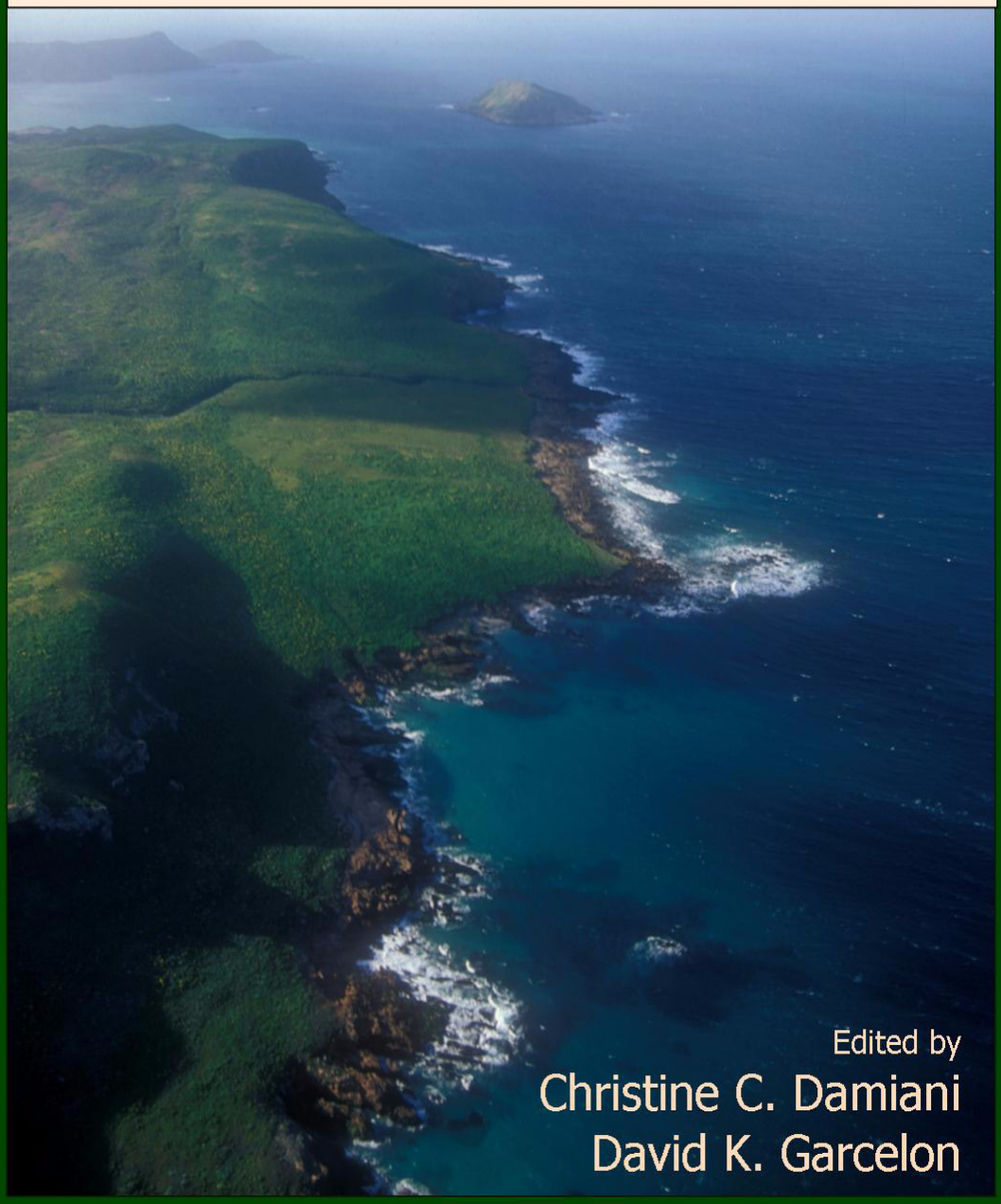
Proceedings of the Seventh California Islands Symposium



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Christine C. Damiani
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Oxnard, California, February 5 – 8, 2008

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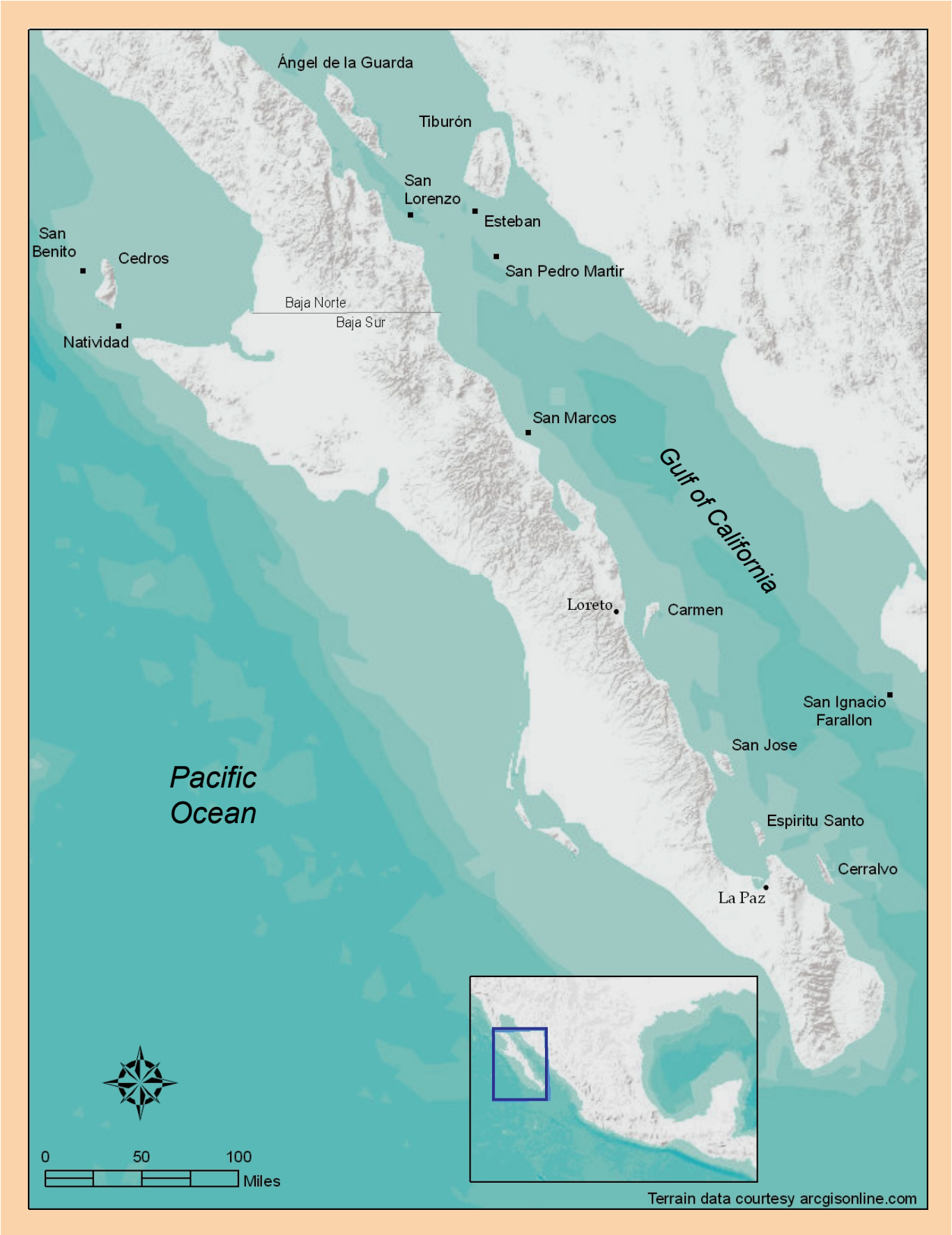
The California Channel Islands and Pacific Baja California Islands



Islands of the Gulf of California

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Preface

The California Islands include the Channel Islands off the coast of southern California, the Pacific Baja California islands, and islands within the Gulf of California. Although most of these islands are situated close to the mainland, they are visited and understood by relatively few of the many people who observe them casually on a daily basis. The seventh California Islands Symposium, held February 5–8, 2008 in Oxnard, California, provided an opportunity for researchers and educators to disseminate their knowledge of the California islands and their surrounding waters. With Santa Cruz Island clearly visible offshore, over 300 participants gathered at the Embassy Suites hotel to attend 154 talks and 28 posters, including a special session on the first five years of monitoring marine protected areas in the Channel Islands. The organizers and participants, ranging from archaeologists and ecologists to geologists and historians, reflected the diversity of stakeholders sharing an interest in these unique islands.

Like most islands, the California Islands are hotspots of biodiversity and extinction. In his keynote address, Dr. Ernesto Enkerlin-Hoeflich stated that although they make up less than 1% of the land area of California and the Baja California peninsula, the Channel and Pacific Baja California islands contain nearly 10% of the region's endemic species and subspecies and have experienced 15% of the region's extinctions, resulting largely from the introduction of invasive plants, large grazers, and non-native predators during the nineteenth and twentieth centuries. Since the last symposium in 2003, heroic efforts have continued in removing these introduced species from the islands, notably the eradication of goats from Guadalupe Island, pigs from Santa Cruz Island, and black rats from San Ignacio Farallón and San Pedro Mártir islands. Thus, a highlight of this meeting was the large number of presentations detailing how the islands' ecosystems have responded to these species' removals. An encouraging number of projects documented success, including the reintroduction of island foxes to San Miguel and Santa Rosa islands, new recruitment of Guadalupe cypress on Guadalupe Island, and increases in native shrub cover on Santa Rosa, San Miguel, and Santa Barbara islands. Other studies pondered why species like the island scrub oak on Santa Catalina Island have not responded as expected to the removal of feral goats and pigs. The presentations also brought forward new and exciting information on prehistoric settlement patterns and indigenous strategies for utilizing island resources, as well as the culture and exploits of the islands' more recent occupants.

These proceedings are a collection of peer-reviewed papers based on a sample of presentations from the symposium. They cover a variety of subjects, ranging from the formation and natural history of the islands to the relationships that prehistoric islanders developed with their environment, and from the history of the ranches that were so influential in shaping the islands' recent history and landscape to current efforts to restore island ecosystems to their natural state. The papers in these proceedings represent ongoing research on the California Islands, which strives to illuminate understanding of an enigmatic landscape rich in history and biodiversity.

Acknowledgments

The Seventh California Islands Symposium was sponsored by a collection of agencies, non-profit organizations, and academic institutions, whose diversity reflects the myriad resources of the islands themselves. In particular, we would like to thank the members of the organizing committee: Shauna Bingham, Julie Bursek, Tim Coonan, Carlos de la Rosa, Kate Faulkner, David Garcelon, Michael Glassow, Ann Huston, Lyndal Laughrin, Danielle Lipski, Yvonne Menard, Fred Piltz, and Catherin Schwemm. Additional assistance for the conference was provided by Emily Dekker-Fiala and the George Wright Society, and by John Brooks, John Curwen, Aura de Anda, Bill Faulkner, Ulysses Huerta, Dick Johnson, Cindy Leon, Carol Peterson, Tina Reed, and Rocky Rudolph.

Financial support for the symposium and proceedings was provided by Minerals Management Service, the NOAA Channel Islands Marine Sanctuary, the Montrose Settlements Restoration Program, the National Park Service California Mediterranean Research Learning Center, the Santa Cruz Island Foundation, the Sea Grant Program of the University of Southern California, Channel Islands National Park, and the Institute for Wildlife Studies.

The editors thank Tim Coonan, Julie Young, and the many anonymous reviewers whose time and feedback enhanced the quality of papers in the proceedings and helped our authors present their research in the best manner possible. In particular, Tim provided us with valuable guidance and moral support throughout this entire process. Dick Johnson assisted with the cover design, and Rocky Rudolph assisted with generating the maps of the California Islands. Finally, we thank Megan Potter, whose patience, diligence, and keen editorial eye were very much appreciated in the final stages of editing and layout.

Christine C. Damiani
David K. Garcelon

October 2009

PREHISTORY

Pages 3–14 in Damiani, C.C. and D.K. Garcelon (eds.). 2009. Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.

THE ORIGIN AND PALEOCLIMATIC SIGNIFICANCE OF CARBONATE SAND DUNES DEPOSITED ON THE CALIFORNIA CHANNEL ISLANDS DURING THE LAST GLACIAL PERIOD

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Abstract—Most coastal sand dunes, including those on mainland California, have a mineralogy dominated by silicates (quartz and feldspar), delivered to beach sources from rivers. However, carbonate minerals (aragonite and calcite) from marine invertebrates dominate dunes on many tropical and subtropical islands. The Channel Islands of California are the northernmost localities in North America where carbonate-rich coastal dunes occur. Unlike the mainland, a lack of major river inputs of silicates to the island shelves and beaches keeps the carbonate mineral content high. The resulting distinctive white dunes are extensive on San Miguel, Santa Rosa, San Nicolas, and San Clemente islands. Beaches have limited extent on all four of these islands at present, and some dunes abut rocky shores with no sand sources at all. Thus, the origin of many of the dunes is related to the lowering of sea level to ~120 m below present during the last glacial period (~25,000 to 10,000 years ago), when broad insular shelves were subaerially exposed. The exposed island shelves probably hosted abundant sand-sized skeletal debris of marine organisms that accumulated during high sea stands of the previous interglacial periods. The carbonate-rich dunes of the Channel Islands are thus a product of an island setting and dramatic sea-level lowering during the last glacial period.

INTRODUCTION

Sand dunes dominate landscapes over a significant portion of the Earth's surface. Although the Earth's largest dune fields are found in arid and semiarid zones of continental interiors, many dunes are also found along the world's coastlines. River transport and wave erosion of bedrock produce a steady supply of loose, sand-sized particles that are readily deflated from beaches by wind to form dunes. Along the Pacific Coast of North America, from Washington to Baja California, dune fields are an intermittent, but important, component of the coastal geomorphology (Cooper 1958, 1967). Sand dunes are found on a number of the California Channel Islands, covering large portions of San Miguel and San Nicolas islands and smaller parts of the northern or northwestern coasts of Santa Rosa, San Clemente, and Santa Cruz islands. Dunes on the Channel Islands display white or grayish-white colors that are distinct from mainland California dunes, which are typically light brown or tan. In this paper, we present new information on the composition of Channel Islands dunes that explains their white color. We also present new field observations that help explain when dune formation occurred and how this is related to sea level change during the last glacial period.

METHODS

Sand dunes were studied primarily on San Nicolas, San Clemente, and San Miguel islands, and secondarily on Santa Rosa and Santa Cruz islands (Fig. 1). To establish relative ages of surficial deposits, we re-mapped the extent of eolian sand and other Quaternary deposits on western San Nicolas Island, using aerial photographs as a mapping base (Fig. 2). Representative samples of

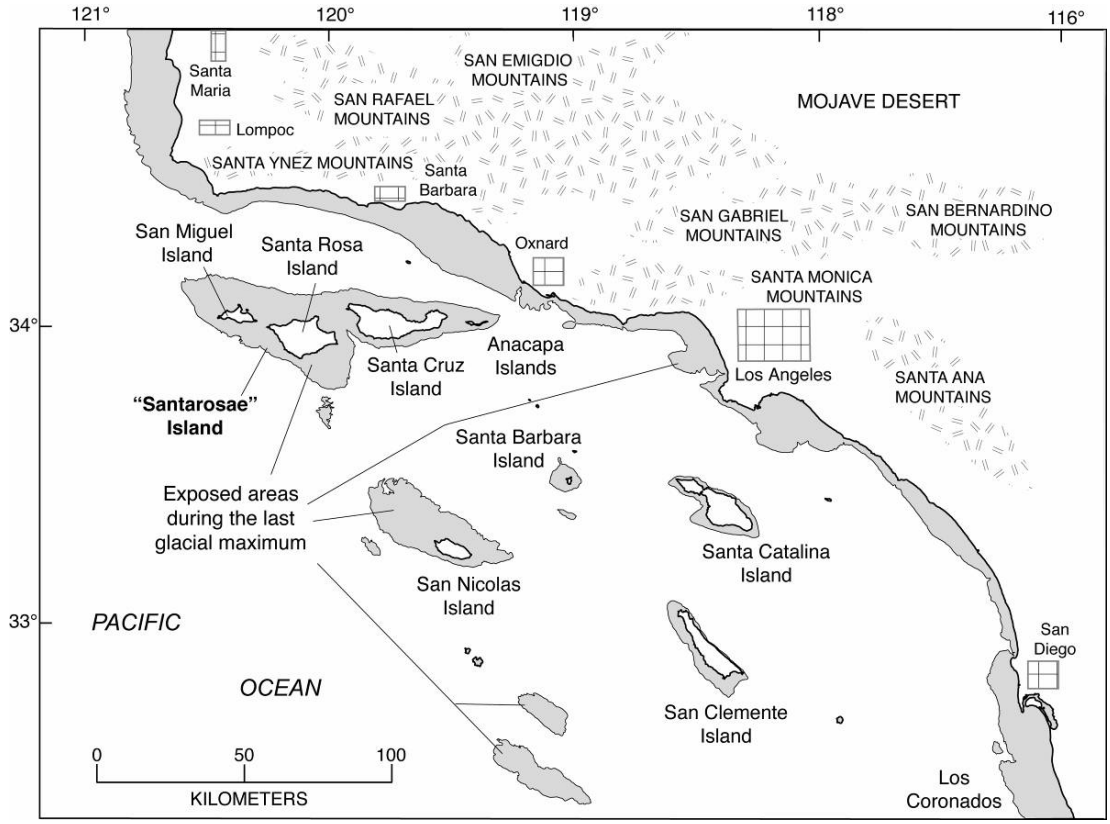

Figure 1. Map of the California Continental Borderland and the Channel Islands. Also shown (gray shading) is the area of now-submerged continental and insular shelves that would have been subaerially exposed during the last glacial maximum, at ~21,000 cal yr BP. Extended land area drawn by the authors using 1:250,000-scale USGS topographic maps, assuming a last-glacial-maximum sea level of ~120 m below present (Fairbanks 1989; Bard et al. 1990).

modern and Pleistocene dunes were collected on San Nicolas Island, as well as samples of modern beaches and Eocene sandstone bedrock. At a particularly complete exposure through a dune sequence at Dizon's Ravine (Fig. 2), we described and sampled eolian sand and buried soils at approximately equal-depth intervals. We also collected samples from Pleistocene dunes on San Clemente Island and modern coastal dunes from mainland California, near the cities of Oxnard, Lompoc, and Guadalupe, west of Santa Maria (Fig. 1).

In the laboratory, we determined the relative proportions of quartz, plagioclase feldspar, calcite, and aragonite for all sand samples using X-ray diffractometry (XRD). Exact percentages of quartz, plagioclase and many other minerals cannot be determined from XRD peak heights, but the ratio of XRD peak heights of these minerals compared to carbonate minerals can be used as a measure of relative mineral abundance. Total $CaCO_3$ (both calcite and aragonite) was measured using a rapid and precise method that utilizes automated coulometric titration (Engleman et al. 1985). Although this method does not distinguish calcite and aragonite, it provides very precise estimates of total carbonate content. To determine whether carbonate minerals were derived from marine or terrestrial sources, we measured concentrations of Sr using X-ray fluorescence. This element has relatively high concentrations in seawater and commonly substitutes for Ca in the skeletal mineralogy of both calcite and aragonite-dominated marine organisms. In contrast, carbonate minerals precipitated from terrestrial waters generally have much lower Sr concentrations. Thus, Sr is a proxy for the presence of marine-derived calcite and aragonite.

The mineralogy of San Nicolas Island dunes was compared to previously published data from

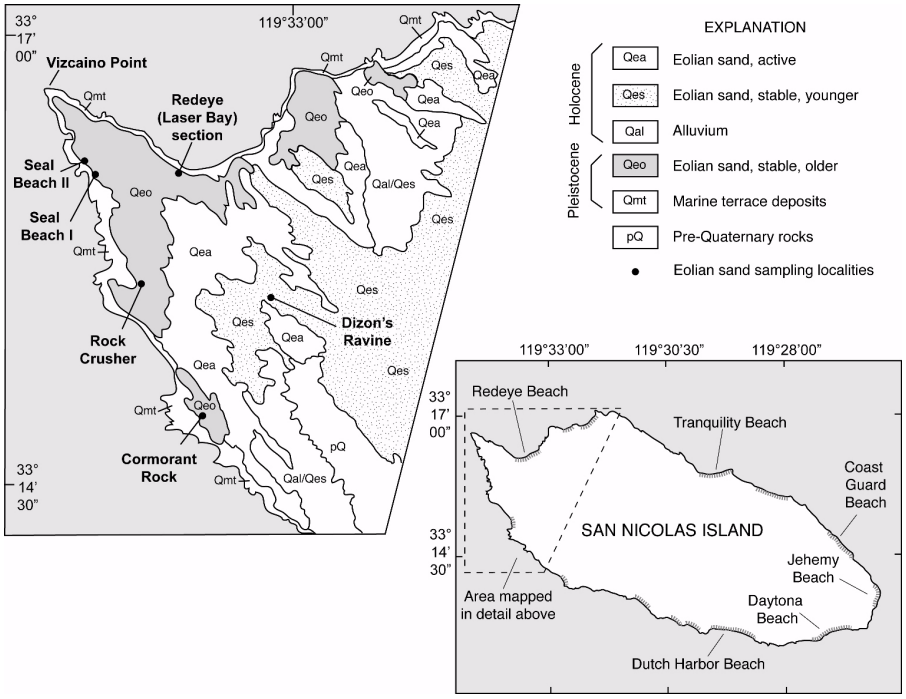

Figure 2: Map showing the distribution of eolian sand and other Quaternary deposits on the western end of San Nicolas Island and localities referred to in the text. Geology by the authors.

desert dunes (Muhs et al. 2003), and to samples collected from mainland California coastal dunes, San Nicolas Island bedrock, and San Nicolas Island beach sand. Ternary diagrams were constructed using the following XRD peaks (all in degrees two-theta): quartz (20.8°), plagioclase (27.8°), aragonite (26.2°), calcite (29.4°). In contrast to the silicate minerals, the separate peaks for calcite and aragonite can be used to determine the proportions of each mineral by measuring peak heights and use of a calibration curve.

RESULTS

Eolian Sand on San Nicolas Island

Eolian (wind-blown) sand is an extensive surficial deposit on San Nicolas Island, particularly in the western part of the island (Vedder and Norris 1963). Although Vedder and Norris (1963) did not distinguish different ages of dunes on their map, they recognized that several ages of eolian sand were present. In our remapping of the island, we recognize three different ages of dunes. The oldest dunes ("Qeo") are found at the surface on the northwest coast and are buried by younger dunes in the interior of the island (Fig. 2). They are commonly weakly cemented into "dune rock" or eolianite, display high-angle cross-bedding, and host well-developed soils. These soils have a reddish-brown, clay-rich Bt horizon in their upper parts and a well-cemented Bk horizon ("calcrete," or "caliche") in their lower parts, although many soils are partially eroded. Based on the degree of soil development, we infer that these dunes are Pleistocene. Younger dunes ("Qes") are stabilized by vegetation, and have minimally developed soil profiles. Commonly, these eolian sands overlie the older deposits, such as in the area around Dizon's Ravine (Fig. 2). These dunes are probably Holocene. The youngest dunes ("Qea") are those that have little or no vegetation, have no soils developed in their upper parts, and experience active transport by wind. Both Pleistocene and stable Holocene dunes host significant numbers of fossil land snails that have been studied in detail by Pearce (1990, 1993). *Micrarionta*, common in the dunes (e.g., Fig. 3), is an island endemic.

Primary and secondary structures in the Pleistocene dunes on San Nicolas Island give

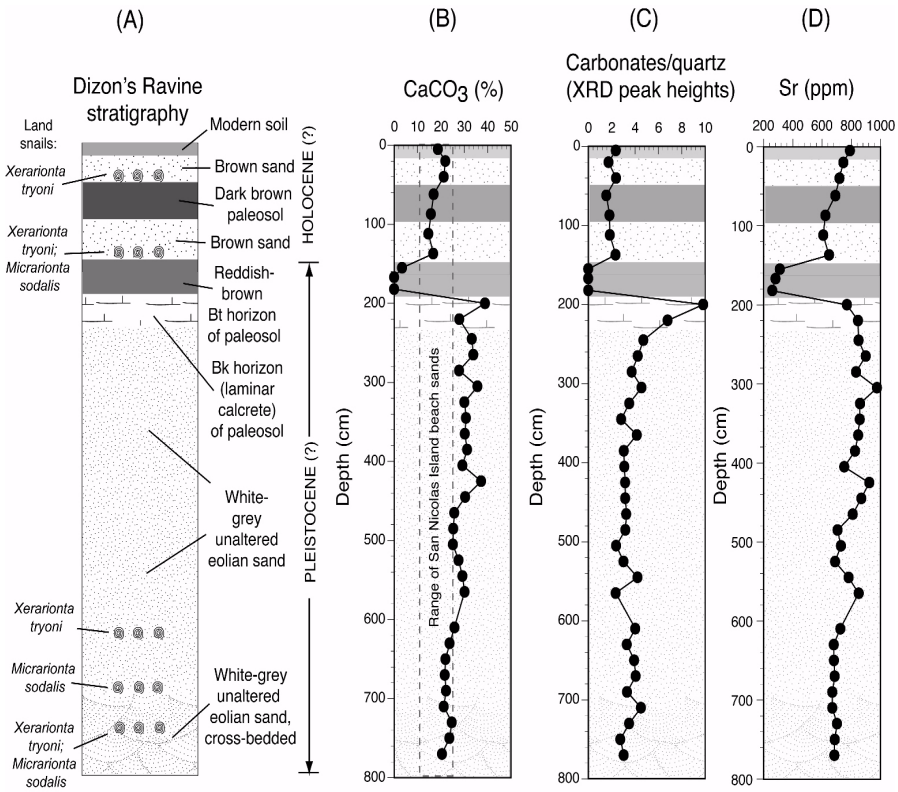

Figure 3. (A) Stratigraphy and land snail species, (B) $CaCO_3$ content, (C) calcite+aragonite/quartz values (based on XRD peak heights), and (D) Sr content of eolian sand and paleosols exposed in Dizon's Ravine, San Nicolas Island (see Figure 2 for location).

important clues about dune history. Exposures of the lowest, older parts of the dunes commonly exhibit high-angle cross-bedding, typically dipping from 25° to 35° to the south, south-southeast, or southeast. The upper parts of many Pleistocene dunes commonly display rhizoliths, or carbonate-filled root, trunk or stem casts of plants. In many exposures, rhizoliths are found in the original plant growth position, but are surrounded and/or buried by eolian sand, indicating deposition was still in progress even when there was at least a minimal plant cover. Eolian sand accretion was likely much slower during this phase of dune deposition, such that vegetation could maintain growth (which in turn probably slowed eolian sand movement). Finally, many exposures of dunes in profile show well-developed soil Bk horizons. Soil Bk horizons do not form when a dune is actively accreting vertically or migrating downwind. Thus, these features represent complete dune stability, colonization by vegetation, and a lengthy period of soil formation.

Composition of Dunes on San Nicolas Island

Microscopic examination of grains in eolian sand from San Nicolas Island shows that although angular-to-subangular quartz is an important mineral, there are large numbers of rounded-to-subrounded skeletal carbonate grains derived from marine organisms. Carbonate grains consist of mollusk shell fragments, sea urchin spines, and other marine skeletal particles. These observations are in broad agreement with more detailed studies conducted by Barron (2003).

Eolian sand exposed in Dizon's Ravine on San Nicolas Island shows how carbonate composition varies in unaltered eolian sand, leached zones of buried soils (paleosols), and enriched secondary calcrete zones of paleosols (Fig. 3). Unaltered eolian sand, whether cross-bedded or unstratified, has between ~20% and ~37% $CaCO_3$. In contrast, horizons of the modern soil and the first buried soil (paleosol) have 15% to 19% $CaCO_3$, and the Bt horizon of the reddish-brown buried soil has only 3% or less $CaCO_3$. The $CaCO_3$ leached from the Bt horizon of the reddish-brown paleosol accumulated

in the Bk horizon of the underlying calcrete, where $CaCO_3$ content ranges from 28% to 39%. These changes in $CaCO_3$ content as a function of depth are mirrored by the ratio of XRD peak heights of carbonate-minerals-to-quartz, and by concentrations of Sr, an index of the abundance of marine-derived carbonate minerals. Measurements of XRD peak heights of calcite and aragonite indicate that of the total $CaCO_3$, 25% to 55% is aragonite and 45% to 75% is calcite. The dominance of calcite over aragonite is in good agreement with the generally higher numbers of calcitic marine organisms vs. aragonitic marine organisms in mid-latitude regions of the ocean (Chave 1967; Nelson 1988).

Mineralogy of San Nicolas Island Dunes Compared with Mainland Dunes

The composition of dune sands on the Channel Islands contrasts strongly with that of mainland desert dunes (Fig. 4A). The most common constituents of inland sand dunes worldwide are quartz and feldspars (see examples in Muhs 2004). Dunes near Parker, Arizona, have high quartz, low calcite, and relatively low plagioclase feldspar content. The Parker dunes are derived primarily from mineralogically mature, quartz-rich sediments of the Colorado River, which are in turn derived from old, quartz-rich sandstones drained by this river on the Colorado Plateau (Muhs et al. 2003). Dunes from Rice Valley, California, in the eastern Mojave Desert lack calcite, and have much higher plagioclase feldspar content relative to quartz. These dunes are derived from local, first-cycle alluvium. In contrast to eolian sands in both of these desert dune fields, San Nicolas Island dunes are relatively low in quartz, high in plagioclase feldspar, and high in carbonate minerals.

San Nicolas Island dunes, both modern sands and those of Pleistocene age, also have a composition that differs from mainland California coastal dunes (Fig. 4B). Samples from dunes near Guadalupe and Lompoc have abundant plagioclase feldspar and quartz. The Lompoc dunes contain no aragonite and only small amounts of calcite; the Guadalupe dunes have no calcite or aragonite at all.

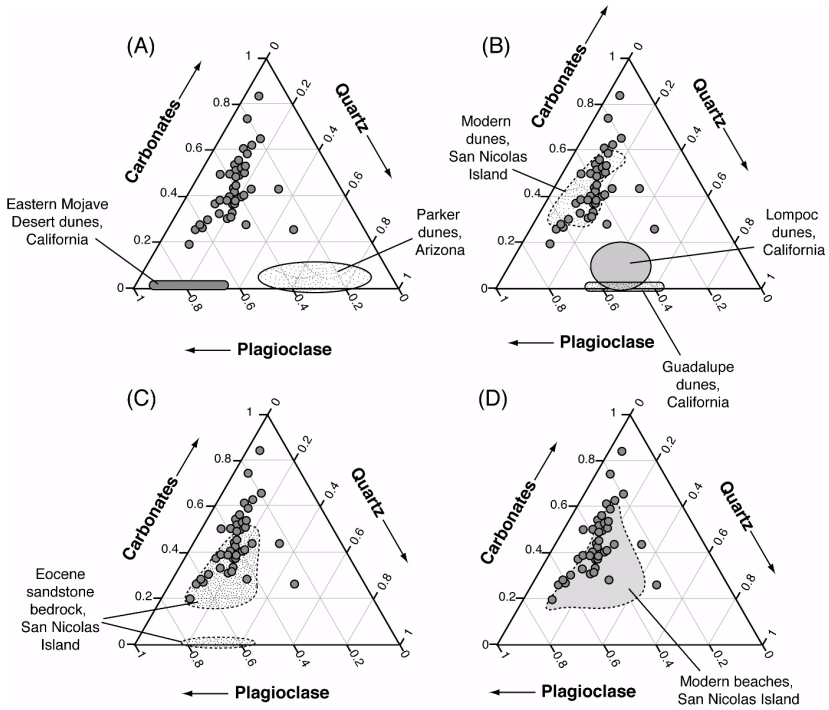

Figure 4. Ternary diagrams comparing relative proportions (*not* percentages) of quartz, plagioclase feldspar, and carbonate minerals (calcite+aragonite) in Pleistocene dunes from San Nicolas Island (filled circles; localities in Fig. 1), with: (A) modern desert dunes (data from Muhs et al. 2003); (B) modern dunes on San Nicolas Island and coastal dunes from mainland California; (C) Eocene sandstone bedrock on San Nicolas Island; and (D) modern beaches on San Nicolas Island.

The actively accreting portions of the mainland California Guadalupe and Lompoc dune fields are derived from nearby beach sediments. These beach sediments are, in turn, derived from sediments delivered to the coast by the Santa Maria and Santa Ynez Rivers (Fig. 5). These rivers drain parts of the southern Coast Ranges (Sierra Madre and San Rafael Mountains) and the western Transverse Ranges (Santa Ynez Mountains). Sandstones and other rocks in these mountain ranges are rich in plagioclase feldspar and quartz (Dibblee 1966; Norris and Webb 1976; Norris 2003) and provide these minerals to the rivers and beaches.

Mineralogy of San Nicolas Island Dunes Compared to Island Bedrock and Beach Sediments

Because San Nicolas Island dunes have much higher calcite and aragonite contents than mainland dunes, it is likely that there is some source of high-carbonate sand that is from the island itself. One possible source of carbonate is the island bedrock. Local bedrock on San Nicolas Island is dominantly Eocene siltstones and sandstones, which contain mostly quartz, plagioclase, and K-feldspar, but also some calcite (Vedder and Norris 1963). Our mineralogical analyses agree with those of Vedder and Norris (1963), with the rocks showing a dominance of quartz and feldspar. Although some of these rocks contain calcite, all lack aragonite and some contain no carbonate minerals at all. A ternary plot comparing the Pleistocene dunes of San Nicolas Island with the Eocene sandstone shows that although there is considerable overlap, most dunes contain a greater abundance of carbonate minerals (Fig. 4C).

In contrast to the Eocene bedrock, San Nicolas Island beach sands have relative abundances of quartz, plagioclase, and carbonate minerals that are

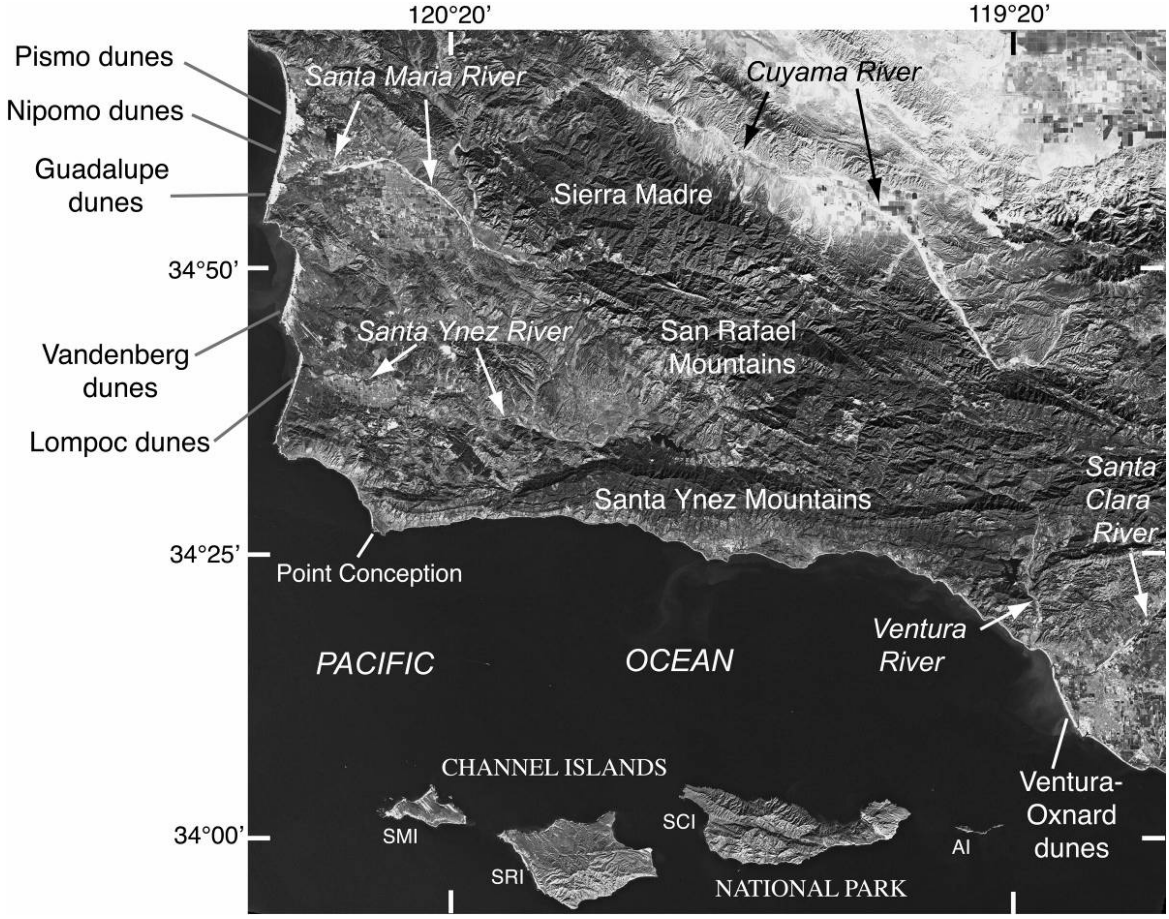

Figure 5. Landsat 7 image (bands 30, 20, and 10) showing the region of coastal southern California from Channel Islands National Park north to the Santa Maria River and coastal mountains. Also shown are the most extensive mainland California coastal dune fields. SMI, San Miguel Island; SRI, Santa Rosa Island; SCI, Santa Cruz Island; AI, Anacapa Islands.

close to those of the Pleistocene dunes (Fig. 4D). Quartz and plagioclase in the beach sediments are probably derived from the local Eocene sandstone bedrock. Unlike the bedrock, however, beach sands on San Nicolas Island contain both calcite and aragonite, which are derived from skeletal particles, in turn derived from marine organisms offshore. Modern beach sands have, overall, higher carbonate mineral content compared to the Eocene bedrock.

Total $CaCO_3$ Content of Channel Islands Dunes, Mainland Dunes, and Source Sediments

We also compared total $CaCO_3$ content, obtained by coulometric titration, in island dunes, mainland dunes, and possible source sediments. Pleistocene dunes on San Nicolas Island have a mean $CaCO_3$ content of 35% (Fig. 6). This value is somewhat lower than what Johnson (1972) reported for eolian sands of various ages on San Miguel Island (mean of ~40%), but somewhat higher than a suite (n=58) of Pleistocene eolian sand samples we analyzed from San Clemente Island (mean of ~32%). Eolian sand exposed in Dizon's Ravine has a mean $CaCO_3$ content of 28%, similar to modern and recently stabilized dunes on San Nicolas Island (Qea and Qes units on Fig. 2), which have a mean $CaCO_3$ content of 27%. In contrast, mainland California dunes from the Guadalupe, Lompoc, and Ventura-Oxnard dunes (Fig. 5) all have $CaCO_3$ contents of <1%.

Possible source sediments for the dunes on San Nicolas Island have highly variable $CaCO_3$ contents. Shelf sands (data from Norris 1951) have $CaCO_3$ contents of just under 20% to as high as 100%, with a mean value of ~48%. Beach sands, sampled at Redeye Beach and Tranquility Beach (Fig. 2), have a mean $CaCO_3$ content of 22%. In contrast, the average $CaCO_3$ content of Eocene sandstone bedrock from Celery Creek Canyon on San Nicolas Island is only 7%.

Timing of Dune Deposition

On the Channel Islands, numerous sea cliff exposures of carbonate eolian sand occur in places where currently no sand source exists. For example, sea cliff exposures of eolian sand commonly abut rocky shores where sandy beaches are absent year-round (Fig. 7). Measurements from ~70 dip azimuths of high-angle (25°-35°) foreset beds from dunes on San Miguel, San Nicolas, and San Clemente islands indicate these beds typically dip to the south, south-southeast, or southeast. This suggests that paleowinds that deposited the dunes were from the north, north-northwest, or northwest, where few or no sand sources exist at present. Thus, dunes in such settings must predate the present (Holocene) interglacial period.

Stratigraphic observations on the Channel Islands support the concept of eolian sand deposition during the last glacial period. Eolian sands exposed on sea cliffs are typically underlain by marine terrace deposits that date to either the early (~120,000 yr BP) or later (~80,000 yr BP) parts of the last interglacial complex (Muhs 1983, 1992; Muhs et al. 2006). This observation constrains the age of the dunes to an interval sometime after the last interglacial period. Well-

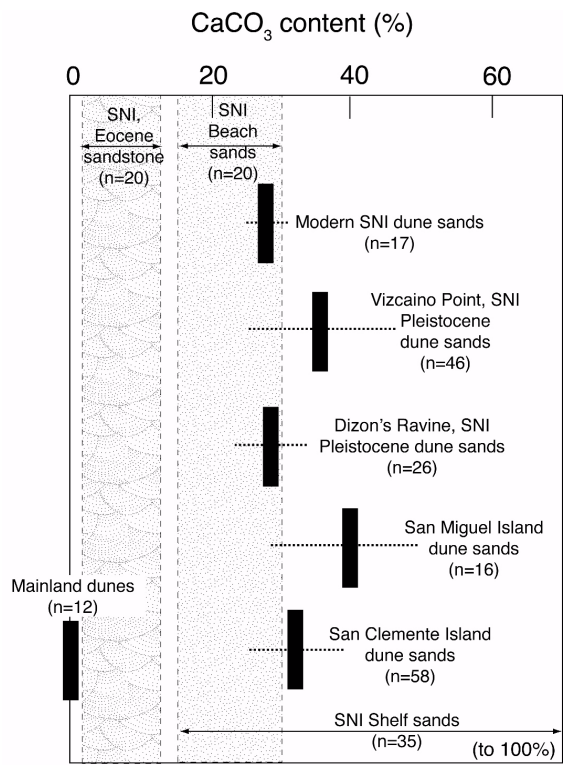

Figure 6. Mean $CaCO_3$ content (thick, black bars; dotted lines are ± 1 standard deviation) of modern and older eolian sands on San Nicolas Island (SNI), and the range of $CaCO_3$ content in various potential source sediments. Also shown is the $CaCO_3$ content of sand dunes on San Miguel Island and San Clemente Island (from locality shown in Fig. 7) and mainland California dunes. All data from this study except those for San Nicolas Island shelf sands, which are from Norris (1951) and San Miguel Island dunes, which are from Johnson (1972).

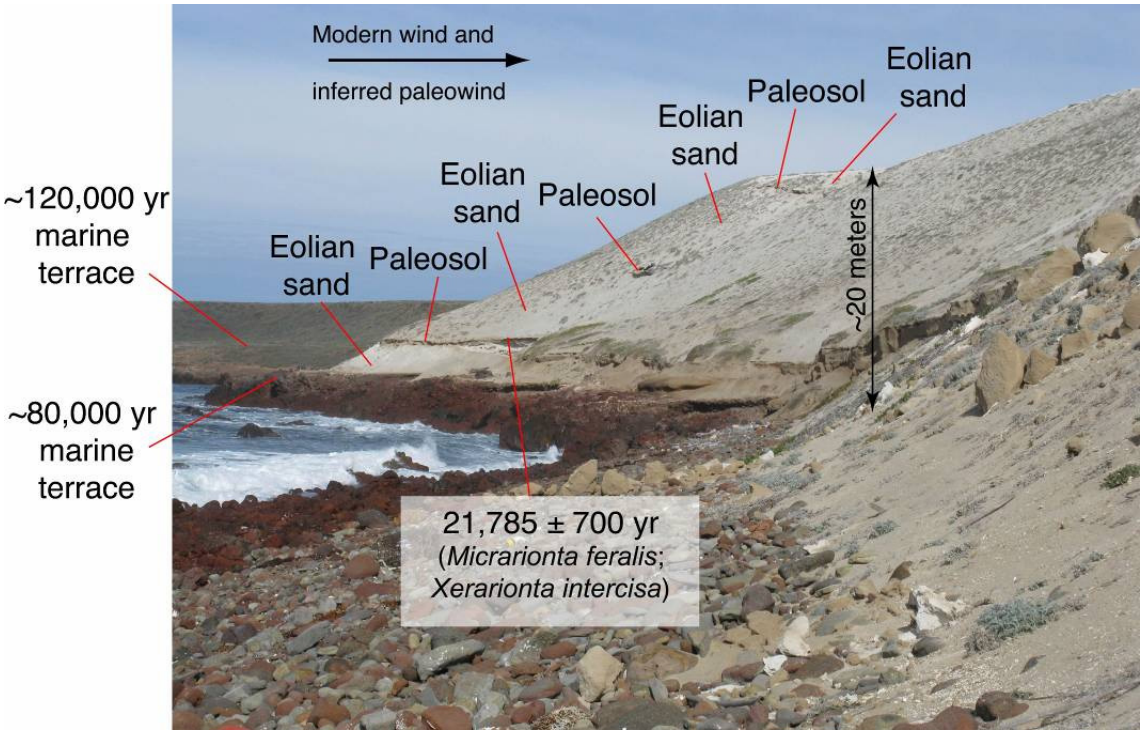

Figure 7. Stratigraphy of eolian sand exposed on the west shore of San Clemente Island (N33°00.046'; W118°34.971'), showing full-glacial age of major carbonate dune package, based on stratigraphic relations and radiocarbon age of land snails (Muhs 1983). Note lack of sand source on present shoreline.

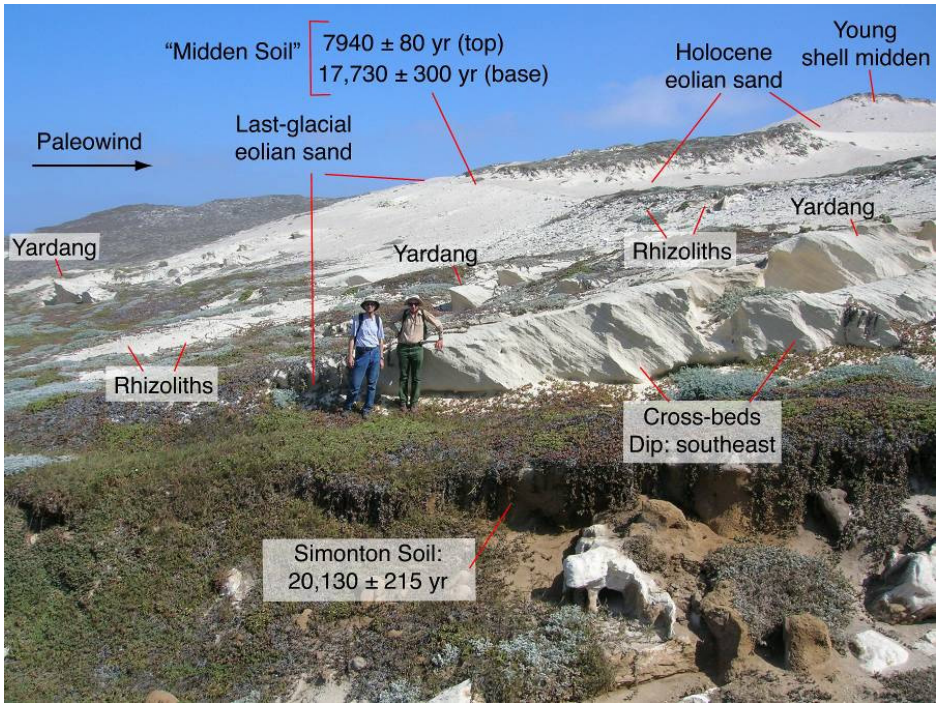

Figure 8. Stratigraphy of eolian sand exposed in Simonton Cove, San Miguel Island, near Yardang Canyon (N34°03.250'; W120°23.083'), showing full-glacial age of major carbonate dune package. "Yardangs" are streamlined landforms carved by the wind and left as erosional remnants. All radiocarbon ages from Johnson (1972, 1977).

developed soils on top of the eolian sands suggest that the dunes did not form during the present (Holocene) interglacial period, narrowing the time period of dune formation to the last glacial period. On San Clemente Island, there is a major dune package, ~20 m thick, that overlies the ~80,000-year-old marine terrace on the west shore (Fig. 7). Land snails (*Micrarionta feralis* and *Xerarionta intercisa*) from a paleosol within this thick dune sequence gave a radiocarbon age of ~22,000 ^{14}C yr BP (Muhs, 1983), very close to full-glacial time. On San Miguel Island, charcoal from a paleosol (the Simonton Soil; Fig. 8) at the base of a thick sequence of eolian sand overlying the lowest (~80,000 yr BP?) marine terrace at Simonton Cove gave a radiocarbon age of ~20,000 ^{14}C yr BP (Johnson 1972, 1977). Another paleosol (the Midden Soil) overlies this dune package, and charcoal from the lower part of this paleosol gave an age of ~17,700 ^{14}C yr BP. These bracketing radiocarbon ages indicate that much of the eolian sand visible in Figure 8 was deposited in just 2000-3000 ^{14}C years during the last glacial period.

DISCUSSION

High Carbonate Production in Waters Outside the Tropics

It is well known that carbonate production along ocean margins is very high in tropical latitudes (James 1997). Hermatypic (reef-building) corals and calcareous green algae dominate carbonate production in warm waters of tropical ocean margins. Consequently, there are many carbonate-rich dunes found along tropical and subtropical coastlines where reefs supply skeletal carbonate sand to beaches and shelves (Gardner 1983; McKee and Ward 1983; Brooke 2001). Nevertheless, there are also areas where carbonate production is significant in higher latitudes, such as the Channel Islands. Thus, the concept of "cool-water carbonates" has arisen within the marine sedimentology community (Chave 1967; Lees and Buller 1972; Nelson 1988; James 1997). Carbonate-producing organisms in cool-water environments include mollusks, foraminifers, echinoderms, bryozoans, barnacles, ostracods, sponges, worms, coralline (red) algae, and ahermatypic corals. All of these marine organisms live off the Channel Islands today and did so in the past as well (for example, see faunal lists in Muhs et al. 2006). Submarine shelves with rich accumulations of cool-water carbonate sediments, similar to the Channel Islands, have been identified off the coasts of New Zealand (Nelson et al. 1988), Vancouver Island (Nelson and Bornhold 1983), and Ireland (Scoffin and Bowes 1988), as well as other localities. Investigators who have studied these environments emphasize that one of the most critical factors in the high carbonate content of the shelves of these non-tropical islands and bank tops is lack of river input from non-carbonate, terrigenous sources. A similar situation exists on the California Channel Islands.

If high carbonate production is not limited to island shelves in tropical waters, a question that arises is why the carbonate dunes on the Channel Islands are so unusual in North America. With high carbonate production found on shelves in mid-latitude and high-latitude waters, at least in those areas where shelf sediments are not diluted by terrigenous silicate particles, it is reasonable to ask why there are not more reports of carbonate dunes on islands outside of the tropics. Gardner (1983) and Brooke (2001) have compiled reports of scattered occurrences of carbonate dunes in England, Ireland, and Scotland. Such dunes are rare, however, and Gardner (1983) speculates that lack of carbonate dunes in high latitudes is likely due to post-depositional dissolution of carbonate grains in climates that are characterized by generally higher precipitation, aided by vegetation that produces

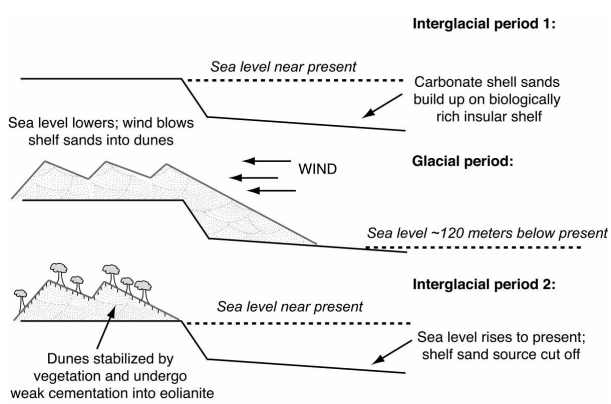

Figure 9. Model of carbonate dune formation as a function of interglacial-glacial cycles and sea-level change on the Channel Islands.

abundant organic acids. The Channel Islands, however, have arid to semiarid climates. Carbonates, though leached to shallow depths in soils and paleosols (Fig. 3), are not completely removed in the dunes.

Carbonates on Mainland vs. Insular Shelves off California

Emery (1960) showed that the $CaCO_3$ contents of shelf sands off the Channel Islands are much higher than those off the mainland California shelf. For example, off the mainland coast near Santa Barbara, $CaCO_3$ contents of shelf sediments range from 1% to 4% and most are only 1% to 2%. In contrast, around Anacapa Island, only 30-40 km to the southeast, $CaCO_3$ contents of shelf sediment range from 10% to 80% (Scholl 1960). The difference in $CaCO_3$ content of sediments on the mainland offshore shelf vs. the island shelves is due primarily to the difference in the relative amounts of delivery of detrital silicate particles vs. production of carbonate skeletal particles (Emery 1960; Johnson 1972). Although skeletal carbonate particle production from marine invertebrate organisms is high adjacent to both the islands and mainland California, in part due to proximity to upwelling cells, mainland shelves receive a greater amount of non-carbonate detrital particles from rivers and streams that drain the coastal mountain ranges (Fig. 5). This detrital silicate (quartz and feldspar) particle input effectively "dilutes" the skeletal carbonate particle input from marine organisms on the mainland California offshore shelf.

In contrast, the Channel Islands have smaller land areas, and, in particular, smaller land areas with any mountainous terrain. Thus, the delivery of detrital silicate particles to island beaches and shelves is commensurately lower. The high carbonate content of insular shelves is well illustrated on San Nicolas Island. Shelf sands off San Nicolas Island have $CaCO_3$ contents that range from 20% to 100% (Norris 1951), far higher than the mean $CaCO_3$ content of sediments on the mainland California shelf, which averages only ~9% (Emery 1960).

Dune Sources During the Last Glacial Period

Eolian sand deposition during the last glacial period was possible because sand sources existed then that are absent now. During the maximum of the last glacial period, ~21,000 yr BP, sea level was ~120 m below present (Fairbanks 1989; Bard et al. 1990). At this time, the northern Channel Islands were connected into a larger, single island called Santarosae (Fig. 1). A particularly large area of now-submerged shelf would have been exposed to the northwest of both San Miguel and Santa Rosa islands. San Nicolas Island would have grown to several times its present areal extent, with the largest expanse of extended subaerial exposure occurring to the northwest (Fig. 1). A sand source to the northwest is consistent with the northwesterly paleowinds estimated from cross-bed dip azimuths.

CONCLUSIONS AND A MODEL FOR GLACIAL-AGE EOLIAN SAND DEPOSITION ON THE CALIFORNIA CHANNEL ISLANDS

The relatively high carbonate content of Channel Islands dunes is rare in North America. Although carbonate-rich dunes, commonly cemented into eolianite, are found on many coastlines, they are unusual outside of tropical and subtropical zones. In North America, excluding Caribbean and western Atlantic islands, carbonate dunes are known to occur only along the Yucatan Peninsula and Baja California, and at one inland locality, Great Salt Lake (McKee and Ward 1983). The high carbonate content of Channel Islands dunes is visually striking to island visitors and often reminds them of tropical islands. The Caliche Ghost Forest of San Miguel Island, a major attraction in Channel Islands National Park, is directly related to the high-carbonate dunes that host it and supplied the carbonate to form the large root and trunk casts (Johnson 1967).

Our findings, and those of Johnson (1972) and Muhs (1992), suggest a three-stage model for carbonate sand accumulation on the California Channel Islands (Fig. 9). During an interglacial period, skeletal carbonate sands build up on biologically rich insular shelves. Lack of terrigenous sediment input from large rivers keeps the carbonate content high. As sea level lowers during the shift into a glacial climate, these shelf sands are exposed and become susceptible to eolian entrainment and transportation. Dunes are built on the subaerially exposed shelf and parts of the

islands. New sediment is no longer exposed when the glacial maximum is reached and sea level lowers to its minimum point. As the glacial period ends and sea level rises (sometimes rapidly; see Fairbanks 1989), some dunes are eroded by the rising sea. Those dunes far enough inland to escape marine erosion have no new supplies of sand, and may undergo stabilization by vegetation, weak cementation to eolianite, and pedogenesis. Rhizoliths record this early vegetation colonization, and pedogenic calcretes record long-term dune stability. Many carbonate-rich dunes on the Channel Islands are, therefore, relict features from the ice ages, and reflect the influence of continental ice sheet growth and effects of this growth on global sea level.

ACKNOWLEDGMENTS

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MAMMUTHUS EXILIS FROM THE CALIFORNIA CHANNEL ISLANDS: HEIGHT, MASS, AND GEOLOGIC AGE

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Abstract—It can be demonstrated that *Mammuthus exilis* was present, in its normal size range, for at least the temporal period of ca. 200,000 to 11,000 years ago. Columbian mammoths (*Mammuthus columbi*) were also present, in lesser numbers, during that time span. In 1990, Louise Roth calculated body mass of island mammoths using the humerus and femur of two *M. exilis* individuals. At that time she was limited to using only museum specimens, due to the policies of the land owners on Santa Rosa Island. In 1994, we excavated the most complete specimen of *M. exilis* yet recovered. Beginning that winter, a pedestrian survey, searching for mammoth remains, was initiated. The survey was controlled by GPS (Global Positioning System) data entry for locations. The survey was conducted through 2008, producing more than 380 localities for mammoth remains on the islands of San Miguel, Santa Rosa, and Santa Cruz. Using specimens collected during these surveys, plus the donation of materials collected by the ranch families, the Los Angeles County Museum, and the Orr collections housed at the Santa Barbara Museum of Natural History, new and expanded interpretations and inferences are provided. The temporal range of island mammoths' residency has been expanded, plus the maximum size of *M. exilis* is considerable less than reported in earlier literature.

INTRODUCTION

The origin of island mammoths (*Mammuthus exilis*) was initially thought to have been derived from *Mammuthus imperator* (Osborn 1942; Hooijer 1976). However, a reassessment has placed 'primitive *M. imperator'* as conspecific with *Mammuthus meridionalis*, and 'advanced *M. imperator'* with *M. columbi* (Agenbroad 2003). Don Johnson (1978) concluded that *M. exilis* was derived from *M. columbi*, as did Madden (1977, 1981).

There have been multiple references to the occurrence of three sizes of mammoths on the Channel Islands (Stock 1935; also cited in Orr 1968 and Roth 1990) that stood, "up to 8 or 9 feet tall at the shoulder". Orr (1968) even suggested there were multiple species of small mammoths on the islands. Stock and Roth had very limited data from which to draw their conclusions. Roth used museum collections, as at that time the islands were private and access was limited. Phil Orr had obtained access to the islands and collected a greater mass of osteological material, but there is no record he used it quantitatively.

Prior to the 1994 discovery of a nearly complete skeleton (Agenbroad et al. 1995), this unique paleontological resource (*M. exilis*) of the California Channel Islands was poorly known. It was decided to analyze the metric attributes of the expanded collection of *M. exilis* specimens to estimate the skeletal shoulder height and body mass of the animals. Additional desired results were determining the total number of mammoth species on the islands, and the temporal range for the species.

METHODS

In 1995 we initiated an ongoing pedestrian survey for mammoth remains. Locations of mammoth remains are recorded with a global positioning system (GPS) (Agenbroad 1998). Collected specimens are housed at the Santa Barbara Museum of Natural History (SBMNH) which also contains the Orr collections. The SBMNH has been designated as the official repository for Channel Islands National Park (CHIS) paleontology. In addition, there was the

extensive osteological collection from Santa Rosa Island, amassed by Boris Woolley, and donated to the SBMNH after his death.

Using the combined osteological collections from the SBMNH and the Los Angeles County Museum (LACM), there is sufficient material for body mass calculations and shoulder heights for a dozen individuals, using both humeri and femora from each individual. Shoulder height of *M. exilis* is calculated from the humerus length, using Harington et al. (1974) methodology. Body mass (weight) has been calculated from both humeri and femora lengths, using equations cited in Roth (1990), from earlier studies.

RESULTS

Shoulder Height

Table 1 and Figure 1 summarize the data for 12 complete humeri specimens. These data provide a skeletal shoulder height range from 1371–1929 mm. All specimens had fused articular surfaces, indicating that they were mature individuals, and reflect probable differences in age and gender. The mean skeletal height for 12 individuals is 1717 mm. These results are in contrast to the, "8- to 9-foot 'intermediate' forms," cited by earlier researchers (Stock 1935; Orr 1968; Roth 1990).

One humerus used by both Stock (1935) and Roth (1990) measured 833 mm in length, giving estimates of an individual with a 2750 mm shoulder height. In the opinion of this author, it is more likely that it falls within the range of a small (female) Columbian mammoth. Both species were found on the islands (ca. 90% *M. exilis* to 10% *M. columbi*) (Agenbroad 1998). Using the Columbian mammoth population at the Mammoth Site of Hot Springs, SD as an example (Agenbroad and Mead 1994), the smallest humerus yet recovered from a minimum of 56 individuals of adolescent to adult, male mammoths is 1000 mm. A humerus of 833 mm is only 167 mm (16.7%) less than the smallest *M. columbi* at Hot Springs, which is well within the estimated 25% size difference due to female/male sexual dimorphism. The 1000 mm South Dakota specimen is 344 mm (34.4%) greater than the longest island mammoth humerus used in this study. That value exceeds the estimated difference due to sexual dimorphism.

Body Mass

Using humeri data (n=12), the mass for *M. exilis* is calculated to range from 380 to 949 kg with an average of 714 kg (Table 1, Fig. 2). Using a different equation, as calculated using femur length, mass is slightly greater: 516 to 1151 kg (Table 2, Fig. 2). The average mass for 12 individuals based on calculations using femora is 759 kg. Roth (1990) states that based on data from living elephants, the femur length calculation is the more appropriate metric for determining mass. Plotting mass from both the humeri and the femora length (Fig. 2), there is an overlap of calculated masses, with 83% of the individuals falling between 500 kg and 950 kg.

Temporal Range

Fully developed *M. exilis* remains are known from the basal conglomerates of the Pleistocene Santa Rosa Island Formation. That geologic unit was dated by Uranium/Thorium (U/TH) at > 200,000 years ago (Orr 1968), and *M. exilis* remains are found to the upper 10 cm of the modern surface. It must be remembered that the existing islands are

Table 1. *Mammuthus exilis* humeri calculations for mass and skeletal shoulder height. ~ indicates that no repository number was listed on the specimen.

Specimen #	Length (mm)	Mass (kg)	Shoulder ht. (mm)
~	606	767	1782
231	466	380	1371
185	621	820	1826
48/48	637	877	1873
94	651	930	1914
6/96	525	523	1544
231 (?)	484	421	1423
CIT-173	530	536	1559
67790	560	621	1647
193	632	858	1859
8/94a	656	949	1929
8/94b	639	884	1879
Mean	584	714	1717
Range	466–656	380–949	1371–1929

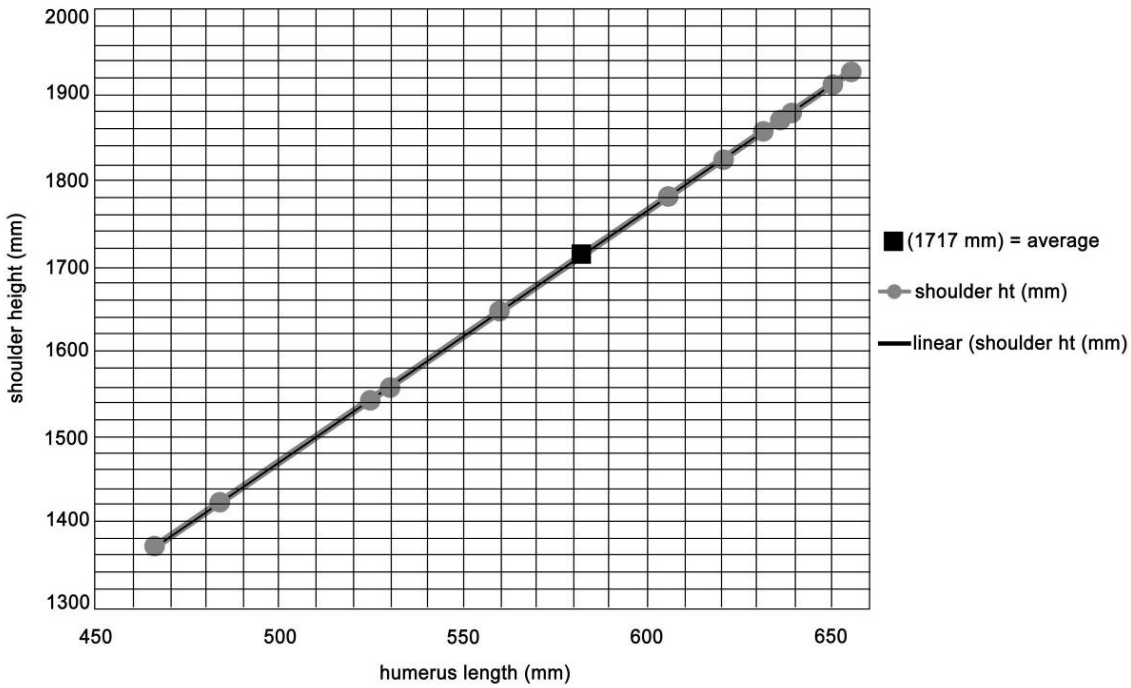

Figure 1. Skeletal shoulder height versus humerus length for *Mammuthus exilis*.

the uplands of the ancient Pleistocene island of Santarosae (Orr 1968). As much as 76% of the Pleistocene island has been inundated by post-Pleistocene eustatic sea level rise (Agenbroad 1999). The conclusion is that *M. columbi* initially (and perhaps periodically) colonized the Pleistocene island, Santarosae. Shortly after colonization, the island selected for smaller forms, and quickly formed the island pygmy mammoths. Sondaar (1977) concluded that island forms reach a reduced size quickly and endure until extinction. Once the Santarosae island form (*M. exilis)* was established, it remained, essentially unchanged until the youngest radiocarbon date of 11,030 yr BP (CAMS-71697), contemporary with the arrival of humans (Agenbroad et al. 2005) as evidenced at Arlington Springs, on Santa Rosa Island (Johnson et al. 2002).

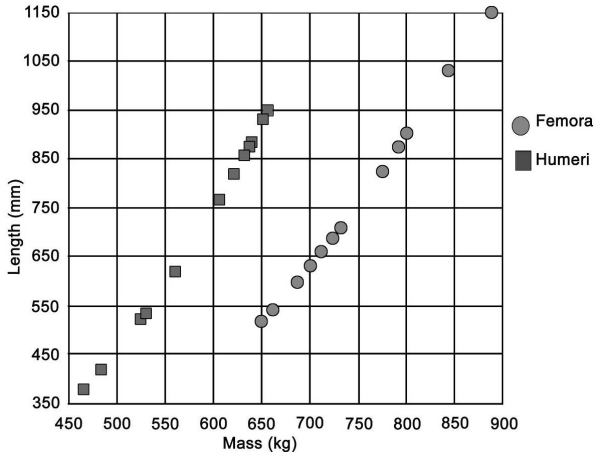

Figure 2. Mass (kg) versus length (mm) for humeri and femora for *Mammuthus exilis*.

SUMMARY AND CONCLUSIONS

Using the data provided by at least 12, each, of humeri and femora of the island mammoths, it can be demonstrated that there are only two species of mammoths on the California Channel Islands: *M. columbi*, the continental mammoth, and *M. exilis*, the island mammoth. Using these data it can further be concluded that *M. exilis* did not exceed 1929 mm in skeletal shoulder height, or more than 949 kg in weight. Average values for skeletal shoulder height and weight are 1717 mm, height (from humeri data, Table 1), and 759 kg in mass (from femora data, Table 2), respectively. Using Table 1, it can be stated that for island mammoths ranging between

Table 2. *Mammuthus exilis* femora calculations for mass.

Specimen #	Length (mm)	Mass (kg)
1947	886	1151
SMICR	661	541
306	842	1029
209b	723	687
209c	700	630
d1	731	708
d2	649	516
6/96	686	598
WC1	774	823
WC2	711	658
8/94a	791	873
8/94b	800	899
Mean	746	759
Range	649–886	516–1151

1400 and 1900 mm in skeletal shoulder height, each increase of 100 mm in height equates to ca. 100 kg increase in mass. It also appears that *M. exilis* was resident on the island(s) from ca. 200,000 U/T years ago until human arrival, at 11,030 radiocarbon years ago (Agenbroad et al. 2005).

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8000 YEARS OF HUMAN SETTLEMENT AND LAND USE IN OLD RANCH CANYON, SANTA ROSA ISLAND, CALIFORNIA

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Abstract—Located on Santa Rosa Island's northeast coast, Old Ranch Canyon contains abundant freshwater, and diverse marine and terrestrial ecosystems, including the nearby Skunk Point dune complex, adjacent Torrey Pine Grove, and Abalone Rocks estuary/marsh near the canyon mouth. These and other factors have made the area an attractive location for human settlement for much of the Holocene. Archaeological survey, ^{14}C dating, and small-scale testing in the canyon and adjacent Skunk Point identified 67 archaeological sites, including shell middens, lithic scatters, and a large Chumash village complex. Radiocarbon dates demonstrate that the canyon and surrounding area were occupied for over 8000 years, with Early, Middle, and Late Holocene occupation of the canyon mouth and hilltops/ ridgelines. These data underscore the importance of continued archaeological survey on the Channel Islands to help identify ancient human settlement patterns and land use strategies, as well as the distribution, diversity, and preservation of island cultural resources.

INTRODUCTION

With one of the longest coastal archaeological records in North America (ca. 13,000 calendar years), Santa Rosa Island provides a remarkable setting for investigating human land use, settlement, and subsistence with great time depth. The generally good preservation of Santa Rosa's archaeological sites also allows for relatively high-resolution analyses of cultural and environmental developments. Consequently, Santa Rosa has long attracted the attention of archaeologists, including excavations in the late nineteenth and early twentieth centuries (e.g., Rogers 1929; Heizer and Elsasser 1956), extensive research by Orr (1968) during the 1940s to 1960s, and more recent work by scholars from Channel Islands National Park and a variety of other institutions (Kennett 1998; Erlandson et al. 1999; Johnson et al. 2002; Rick et al. 2005b; Rick et al. 2006; Braje et al. 2007; Rick 2007; Morris n.d.). Despite these research projects, much remains to be learned about the archaeology of Santa Rosa Island, including the island's northeast coast, which is the location of the most intensive National Park Service (NPS) activities and public visitation.

In this paper, I report the results of a recent survey and ^{14}C dating project in the Old Ranch Canyon region of Santa Rosa's northeast coast. Previous research on the east coast has largely been limited to small-scale testing, survey around the coastline, and brief site reports (Kennett 1998; Rick et al. 2005b; Rick et al. 2006; Wolff et al. 2007; Rick 2008). In 2005–2006, all of Old Ranch Canyon was systematically surveyed for cultural resources. The survey results provide insight into the nature of human and environmental dynamics that span over 8000 years. When placed in the context of research elsewhere on the Channel Islands, these data help refine our interpretations of long-term trends in human settlement and land use, providing important context for future research.

CONTEXT AND BACKGROUND

With an area roughly 217 km^2, Santa Rosa Island is the second largest of the northern Channel Islands. It is situated 44 km off the mainland coast, about 5 km east of San Miguel Island and 9 km west of Santa Cruz Island. Santa Rosa contains some of the greatest biological and environmental diversity on the Channel Islands, including a number of relatively well-watered streams, mountain peaks around 475 m high, and several unique vegetation communities. Distinct coastal beach and dune

vegetation, island chaparral, oak and riparian woodland, and an island endemic species of Torrey pine (*Pinus torreyana insularis*) are among the native vegetation on the island.

Native American settlement on Santa Rosa Island spans roughly 13,000 calendar years (Johnson et al. 2002). The number of sites on the island increases considerably after about 10,000 cal BP, with the most dense human occupation of the island occurring during the Late Holocene, especially after about 1500 years ago (Kennett 2005; Rick et al. 2005a). During the last 1500 years, Chumash peoples lived in villages scattered around the northern islands, engaged in extensive exchange networks, and were among the most populous and complex hunter-gatherers known (Arnold 2001; Kennett 2005; Rick et al. 2005a). Although questions remain about some of the locations of these villages, archaeological and ethnohistoric research suggests that there were about 22 Chumash villages on Santa Cruz, San Miguel, and Santa Rosa islands (Johnson 1999; Kennett 2005), including 9 on Santa Rosa.

Old Ranch Canyon is positioned on the east coast between Skunk and East Points and near the Torrey Pine Grove at its western extremity (Fig. 1). Unlike most canyons on Santa Rosa Island, it trends northwest to southeast, has a strategic location close to Bechers Bay and adjacent Santa Cruz Island, and has a fairly broad and flat canyon bottom (Fig. 2). Old Ranch Canyon has a small marsh at its mouth that is adjacent to a similar system at the mouth of Old Ranch House Canyon (Abalone Rocks). Together the drainages at Old Ranch and Old Ranch House Canyon appear to have formed a paleoestuary during the Early to Middle Holocene. The adjacent Abalone Rocks marsh was cored for a paleoecological study, providing one of the few records of ancient landscape changes for the Channel Islands (Cole and Liu 1994; Anderson 2002). Several archaeological sites in and around the canyon contain the remains of estuarine and rocky intertidal shellfish, demonstrating that people used all available habitats and environments. However, we are just beginning to understand the nature of such strategies (Rick et al. 2005b; Rick et al. 2006; Wolff et al. 2007).

Previous archaeological survey in Old Ranch Canyon has been sporadic and includes sites recorded on the northern canyon rim and the canyon mouth (P. Orr, unpublished site records), and along the coast (Morris n.d.). The status and condition of

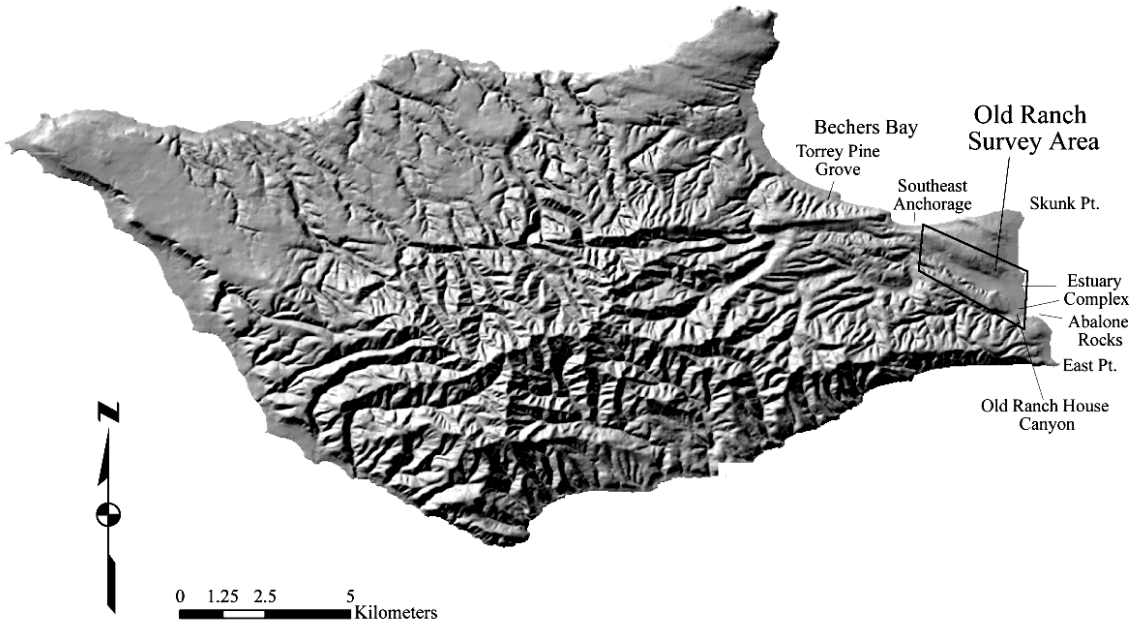

Figure 1. Santa Rosa Island, Old Ranch Canyon survey area, and major areas discussed in the text.

Figure 2. Old Ranch Canyon looking east towards the canyon mouth, showing the broad, flat valley floor and canyon slopes.

the sites at the canyon mouth were also recorded and updated by Rick and Erlandson (2004). The goals of the survey reported here were to identify the nature, extent, and chronology of human use of Old Ranch Canyon, including the importance of a variety of habitats, environments, and landforms in human settlement and subsistence systems.

METHODS

All field and laboratory work was performed by researchers from Southern Methodist University and Channel Islands National Park. These research teams conducted a systematic pedestrian survey for cultural resources in Old Ranch Canyon and adjacent areas of eastern Santa Rosa Island (i.e., Skunk Point, Torrey Pine Grove, and Southeastern Anchorage) from 2005–2006. The Old Ranch Survey area was roughly 4.5 km^2, with additional reconnaissance and sampling in the adjacent Torrey Pine Grove and Skunk Point. We employed standard survey techniques comparable to Kennett (1996), Perry (2004, 2005), and Peterson (1994) with four to five people systematically walking across the landscape and spaced about 3–5 m apart depending on the terrain. Archaeological sites were identified primarily by the presence of artifacts (e.g., chipped stone tools and debitage) and/or ecofacts (shell and bone). Since portions of the Old Ranch Canyon floor are covered with thick deposits of sediment, augers were excavated in some areas of the canyon floor to determine the possibility of buried archaeological deposits, but none were encountered. Archaeological sites were recorded on California State primary and archaeological site records and attachments. The condition, status, and potential of any threats to the cultural resources were also documented using standard NPS criteria (see Rick and Erlandson 2004). All site locations were plotted on topographic maps with the aid of handheld GPS units.

To determine site chronologies, ^{14}C samples (mostly shellfish) were collected *in situ* from trowel probes at all sites with organic materials. Only well-preserved fragments of single shells were selected for dating. All radiocarbon dates presented here were run by the National Ocean Sciences AMS Facility at the Woods Hole Oceanographic Institution or by Beta Analytic Inc., following procedures available at http://nosams.whoi.edu/clients/data.html and http://www.radiocarbon.com/labmethods.htm. All dates were calibrated with CALIB 5.0.2 (Stuiver and Reimer 1993; Stuiver et al. 2005), applying a ΔR of 225 ± 35. We also visited several previously recorded sites in the vicinity of Old Ranch Canyon, Skunk Point, and the Torrey Pine Grove to collect specimens for ^{14}C dating and

Table 1. Archaeological sites in Old Ranch Canyon (newly recorded sites noted with an *).

Site Number	Description	Age (cal BP)
SRI-81	Large shell midden with estuarine and rocky shore taxa	7530–7240
SRI-82	Shell midden with mostly California mussel	2290–1990
SRI-85	Large site with house depressions	920–300
SRI-86	Sparse shell midden near canyon mouth	n/a
SRI-87	Probable village site with glass beads	Historic
SRI-89	Hilltop shell midden with estuarine and rocky shore taxa	6370–6130
SRI-90	Hilltop shell midden with mostly California mussel	3860–3590
SRI-91	Hilltop shell midden with mostly California mussel	3880–3620
SRI-92	Lithic scatter on hilltop	n/a
SRI-93	Hilltop shell midden with mostly California mussel	4370–4040
SRI-189	Small shell midden near beach	n/a
SRI-190	Small shell midden near beach	2640–2320
SRI-191	Dune site with red abalone midden, estuarine shell, and California mussel	6170–4150
SRI-192	Multicomponent site with estuarine shell	6860–2280
SRI-196	Small shell midden near beach	2570–2210
SRI-671*	Small lithic scatter on hilltop	n/a
SRI-672*	Small lithic scatter on hilltop	n/a
SRI-673*	Hilltop shell midden with estuarine and rocky shore taxa	6210–5920
SRI-674*	Small lithic scatter on hilltop	n/a
SRI-675*	Eroding shell midden and lithic scatter on hilltop	1460–1260
SRI-676*	Hilltop shell midden with mostly California mussel	4060–3760
SRI-677*	Small lithic scatter on hilltop	n/a
SRI-678*	Hilltop shell midden with mostly California mussel	2650–2330
SRI-679*	Hilltop shell midden with estuarine/rocky shore taxa and lithic scatter	6400–6130
SRI-680*	Large lithic scatter on hilltop	n/a
SRI-681*	Shell midden on hillside with mostly California mussel	n/a
SRI-682*	Small lithic scatter on hillside	n/a
SRI-683*	Lithic scatter on hillside with two microdrills	Late Holocene
SRI-684*	Large lithic scatter on hilltop with crescent fragment	Early Holocene
SRI-685*	Small lithic scatter on hillside	n/a
SRI-686*	Small lithic scatter on hilltop	n/a
SRI-687*	Shell midden and lithic scatter with estuarine/rocky shore taxa	7690–7500
SRI-688*	Small lithic scatter on hillside	n/a
SRI-689*	Shell midden on hillside with mostly California mussel	n/a
SRI-690*	Deeply buried shell midden exposed in Old Ranch Creek	4800–4520
SRI-691*	Small lithic scatter on hilltop	n/a
SRI-692*	Shell midden just above creek in valley floor with small cave	2000–1730
SRI-693*	Shell midden on hillside with mostly California mussel	n/a
SRI-694*	Shell midden and lithic scatter with estuarine/rocky shore taxa	6400–6160
SRI-695*	Lithic scatter on hillside	n/a
SRI-696*	Small lithic scatter on hillside	n/a
SRI-697*	Shell midden near canyon mouth with mostly California mussel	n/a
SRI-698*	Shell midden near canyon mouth with mostly California mussel	n/a
SRI-699*	Shell midden on hilltop with mostly California mussel	1370–1180
SRI-700*	Large cave with shell midden	1780-1500/Historic
SRI-701*	Small shell midden on valley floor near creek	n/a

bulk midden samples. However, the focus here is on the results of the Old Ranch Canyon Survey, with some of the results of the surrounding research available elsewhere (Rick et al. 2005b; Rick et al. 2006; Wolff et al. 2007).

RESULTS

A total of 46 archaeological sites have been recorded in Old Ranch Canyon, including 31 new sites and 15 previously recorded sites (Table 1). Twenty-one additional sites have been recorded in the adjacent Skunk Point area bringing the total to 67 sites for the Old Ranch/Skunk Point vicinity. For Old Ranch Canyon, this includes 23 shell middens, 15 lithic scatters, 4 shell middens/lithic scatters, 2 caves/rockshelters, and 2 village sites near the canyon mouth. Of the 46 sites identified in the canyon, 29 (63%) were found on the canyon hilltops or higher elevations, including 15 lithic scatters, 13 shell middens, and a cave/rockshelter site. Only one buried site was found in the creek exposures and this was a deeply buried component covered by Late Holocene alluvium. Other than the sites at the canyon mouth, only three sites (CA-SRI-690, -692, and -701) were identified on the interior valley floor. The total number of recorded sites indicates about 10 sites per km^2, a fairly high amount given the fact that vegetation cover was thick and sediments made finding sites on the canyon bottom very difficult.

The contents of the sites were highly variable, including a red abalone midden; numerous sites with estuarine shell; lithic scatters with microdrills, crescents, and other artifacts; and dense middens with a variety of vertebrate and invertebrate faunal remains. In addition to the sites noted here, seven isolates including two Early Holocene crescents and other chipped stone artifacts were identified. Several badly weathered and eroded chert outcrops were also identified. These outcrops consist of fragments of a poor quality, granular chert that is generally an opaque tan or yellowish color. None of these small outcrops were definitive quarries, but lithics from sites in the area suggest that this chert was a source of toolstone (Wolff et al. 2007).

Fifty-one radiocarbon dates were obtained from sites in Old Ranch Canyon and Skunk Point, with a number of other dates available from adjacent areas to the south and west (see Kennett 1998, 2005; Rick et al. 2005b). Radiocarbon dates from Old Ranch range in age from ca. 8180 to 300 cal BP, with glass and/or needle drilled beads at SRI-87 and SRI-700 also demonstrating Historic period occupation (Table 2). Three crescents and an Arena point recovered from the area also indicate an Early Holocene occupation (Rick 2008). These ^{14}C dates and artifacts document a more or less continuous sequence of human occupation through most of the Holocene, including settlement on the canyon mouth, interior, and ridgelines/hilltops (Fig. 3). There are currently two gaps in the distribution of radiocarbon dates in the Old Ranch area with only one site dated between about 3600 to 2700 cal BP and none between a brief period around 7200 to 7000 cal BP. Marine climate records suggest a period of generally cold marine conditions and high marine productivity between about 3600 to 2700 years ago, following a period of generally warm marine conditions and low productivity for most of the Middle Holocene (Kennett et al. 2007). The brief interval between 7200 to 7000 years ago is a time of generally warm marine conditions and low marine productivity that persisted for most of the period from about 7500 to 3800 cal BP (Kennett et al. 2007). These chronological gaps, however, do not correlate strongly with climatic developments and several sites falling in these intervals have been found elsewhere on the northern Channel Islands (see Kennett 2005; Rick et al. 2005a), suggesting that further dating of sites on the east coast of Santa Rosa Island would reveal components dating to these intervals.

DISCUSSION AND CONCLUSIONS

The Old Ranch Canyon survey provides an 8000-year record of human settlement and land use, indicating human use of virtually all available habitats and environments, including the coastline, interior, canyon bottom, hilltops/ridgelines, and two caves/rockshelters. The most substantial sites appear to be Late Holocene village sites located at the canyon mouth, but several other sites also supported human occupation along the coast and/or hilltops throughout much of the Holocene. In contrast to the large numbers of sites along the coast and at higher elevations, only three sites were found

Table 2 . Radiocarbon dates from Old Ranch Canyon and Skunk Point.[1]

Site number	Provenience	Lab #[2]	Material	$^{13}C/^{12}C$ adjusted age	Calibrated age (cal BP, 2 sigma)
SRI-61	Mussel midden, stratum 2	OS-61785	M. californianus	3390 ± 35	3130–2820
SRI-61	Red abalone midden, stratum	OS-61786	M. californianus	5330 ± 35	5570–5330
SRI-61	Deflated estuary midden	OS-59390	O. lurida	6580 ± 40	6960–6680
SRI-76	Auger 1, ca. 55-60 cmbs in situ	OS-61787	M. californianus	4670 ± 35	4800–4480
SRI-77	Unit 2: 50-60 cm	OS-32098	Shell bead	1700 ± 40	1160–920
SRI-77	Col. 1: 40-50 cm	OS-32376	Marine shell	1800 ± 30	1250–1020
SRI-77	Basal midden paleosol, sea cliff	B-180926	C. undatella	7220 ± 90	7660–7310
SRI-81	A3, 40-60 cm	B-109770	Chione sp.	7090 ± 70	7530–7240
SRI-82	Auger 2, 180-20 cmbs in situ	OS-54917	M. californianus	2700 ± 35	2290–1990
SRI-85	Unit 1, 0-10cm	B-96870	H. cracherodii	1060 ± 60	560-300
SRI-85	Unit 3, 0-10 cm	OS-34575	S. bifurcatus	1160 ± 30	630–480
SRI-85	Unit 2, 0-10 cm	OS-34576	S. bifurcatus	1260 ± 70	730–490
SRI-85	Sample A3, Unit 1, 70-80cmbs	B-107044	M. californianus	1270 ± 60	720–510
SRI-85	Sea cliff profile, 120 cmbs	B-100513	M. californianus	1300 ± 80	780–500
SRI-85	Unit 2, 50-72 cm	OS-34574	M. californianus	1500 ± 30	920–710
SRI-89	^{14}C probe 20 cmbs	OS-56420	C. fluctifraga	6050 ± 40	6370–6130
SRI-90	Surface scrape 0-2 cmbs	OS-61788	P. staminea	4010 ± 35	3860–3590
SRI-91	^{14}C probe 0-4 cmbs	OS-60413	M. californianus	4030 ± 30	3880–3620
SRI-93	Midden exposure 0-3 cmbs	OS-60634	M. californianus	4350 ± 35	4370–4040
SRI-155	Deflated estuarine midden	OS-56418	C. californiensis	7660 ± 40	8010–7780
SRI-190	Sea cliff, 50-60 cmbs	OS-54918	M. californianus	2950 ± 30	2640–2320
SRI-191	Mussel/Urchin midden	OS-41895	M. californianus	4450 ± 35	4470–4150
SRI-191	Red abalone midden	OS-37594	C. undatella	5740 ± 45	6050–5730
SRI-191	Red abalone midden	OS-46941	H. rufescens	5870 ± 30	6170–5930
SRI-192	Auger 2, 58-60 cmbs in situ	OS-51720	M. californianus	2920 ± 40	2610–2280
SRI-192	Unit 1 top 10-12 cmbs	OS-54919	S. nuttalli	5670 ± 35	5930–5690
SRI-192	Unit 1, base ca. 60 cmbs	OS-51578	O. lurida	5990 ± 40	6290–6020
SRI-192	South site probe	B-183138	O. lurida	6440 ± 70	6860–6460
SRI-196	Sea cliff 50 cmbs	OS-54920	M. californianus	2900 ± 35	2570–2210
SRI-209	Mound 2, unit 2	B-232734	T. stultorum	4540 ± 60	4650–4230
SRI-209	Mound 1, unit 1	B-232733	T. stultorum	4720 ± 50	4830–4520
SRI-209	Unit 3, mussel midden	B-232735	M. californianus	4950 ± 80	5260–4800
SRI-210	Deflated Pismo clam midden	B-232736	T. stultorum	4630 ± 70	4800–4380
SRI-666	Sample A	B-47626	S. nuttalli	7780 ± 70	8180–7850
SRI-667	Dune 1: Stratum 1	OS-41892	M. californianus	4410 ± 40	4410–4110
SRI-667	Dune 2: Stratum 1	OS-48510	M. californianus	4510 ± 30	4530–4250
SRI-667	Dune 2: Stratum 2	OS-48515	M. californianus	4600 ± 35	4700–4390
SRI-667	Dune 1: Stratum 2	OS-41893	M. californianus	4730 ± 40	4830–4540
SRI-667	Dune 2: Stratum 3	OS-41894	C. undatella	5990 ± 45	6290–6010
SRI-673	^{14}C probe 15-25cmbs	OS-51547	O. lurida	5890 ± 50	6210–5920
SRI-675	^{14}C probe 10-15 cmbs	OS-61782	M. californianus	2020 ± 30	1460–1260
SRI-676	^{14}C probe 15 cmbs	OS-61783	M. californianus	4140 ± 30	4060–3760
SRI-678	^{14}C probe 20-25 cmbs	OS-51548	M. californianus	2970 ± 35	2650–2330
SRI-679	^{14}C probe 10-12 cmbs	OS-51549	C. californiensis	6070 ± 50	6400–6130

Table 2 (continued). Radiocarbon dates from Old Ranch Canyon and Skunk Point.[1]

Site number	Provenience	Lab #[2]	Material	$^{13}C/^{12}C$ adjusted age	Calibrated age (cal BP, 2 sigma)
SRI-687	Deflated estuarine midden	OS-56415	C. californiensis	7350 ± 35	7690–7500
SRI-690	Lowest buried creek deposit	OS-60410	M. californianus	4700 ± 30	4800–4520
SRI-692	^{14}C probe 58-60 cmbs	OS-60633	M. californianus	2490 ± 35	2000–1730
SRI-694	Midden exposure 0-2 cmbs	OS-60411	S. nuttalli	6080 ± 45	6400–6160
SRI-699	^{14}C probe 22-25 cmbs	OS-60417	M. californianus	1950 ± 30	1370–1180
SRI-700	Midden below cave, 40-42 cmbs	OS-51550	M. californianus	2280 ± 40	1780–1500
SRI-702	Sea cliff exposure 50 cmbs	OS-59387	M. californianus	2320 ± 30	1800–1550

[1]All dates were calibrated with CALIB 5.0.2 (Stuiver and Reimer 1993; Stuiver et al. 2005) applying a ΔR of 225 ± 35.

[2]OS=NOSAMS and B=Beta.

on the canyon bottom. The dearth of sites in the canyon bottom is probably largely a result of sediment and dense grass cover obscuring site visibility, but a survey of Wreck Canyon on the south coast of Santa Rosa also noted few sites on the valley bottom (Morris 1993). Early Holocene dates from sites in the adjacent area (SRI-84, -155, and -666) provide further evidence of a ca. 8000 cal BP occupation. It is likely that other early sites have yet to be found, as they may be deeply buried, are badly eroded (this is the case for CA-SRI-666 and -155, both of which are partially deflated), or are submerged offshore.

Other archaeological surveys have indicated that prehistoric human land use and settlement on the northern Channel Islands were highly variable and influenced by the availability of resources in the local environment. On Santa Rosa Island, for

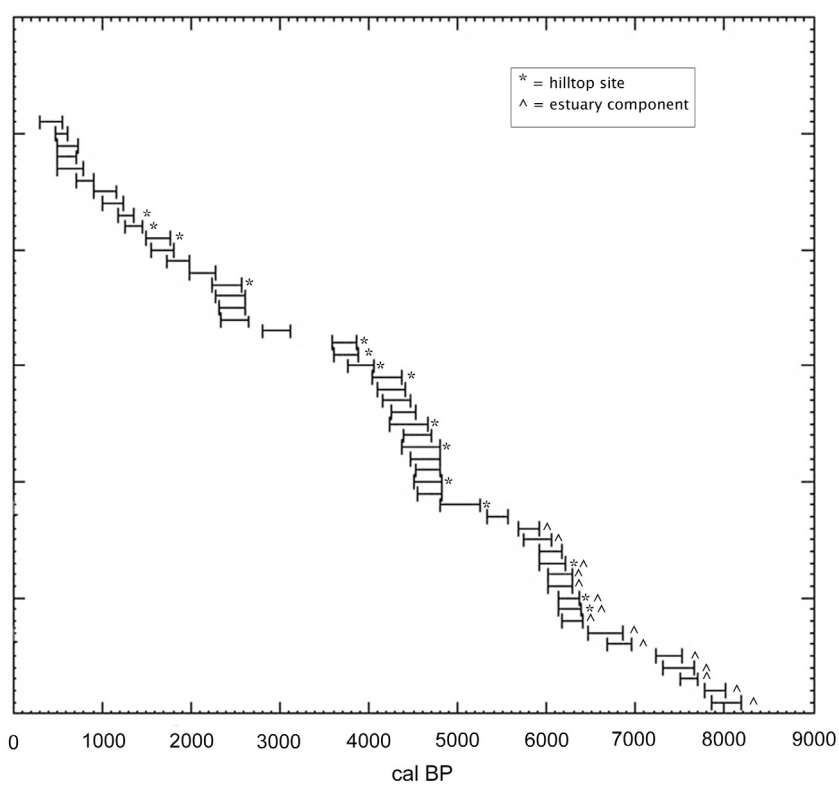

Figure 3. Plot of the 51 calibrated radiocarbon dates (2 sigma) from the Old Ranch Canyon and Skunk Point vicinity, showing the distribution of dated hilltop sites and dates for sites with estuarine shellfish.

example, Morris (1993) identified 34 sites in a 4 km^2 area in Wreck Canyon, with 79% of these associated with a rockshelter and just six sites on the valley floor. In adjacent Jolla Vieja Canyon, York (1996) found that most of the 45 sites identified in the nearly 10 km^2 survey were midden or habitation sites found on stream terraces, although 11 rockshelter sites and numerous lithic scatters were found on ridgetops. Kennett's (1996) survey of lower CanadaVerde on the north coast identified 34 archaeological sites in a 6.5 km^2 area, including a number of hilltop shell middens and lithic scatters and large shell middens at the canyon mouth. Morris's (n.d.) survey of the entire Santa Rosa coastline found a wide variety of site types on the coast, including rockshelters, village sites, shell middens, and lithic scatters. On the south coast of adjacent San Miguel Island, sites dating from 9500 years ago through the Historic period include small rockshelters, large midden deposits, shellfish processing camps, and other site types found on the coast and at the base of the southern escarpment where people may have been getting shelter from northwesterly winds and had better access to freshwater (Braje 2007). On eastern Santa Cruz Island, trans-Holocene settlement data demonstrate substantial movement between the coast and interior and use of hilltops/ridgelines, rockshelters, and chert quarries (Perry 2004). The Old Ranch survey augments these earlier studies by also documenting diverse settlement strategies and occupation of a variety of site types and landforms, including numerous hilltop middens and lithic scatters, and a large Chumash village complex.

Compared to a few other areas surveyed on Santa Rosa, San Miguel, and Santa Cruz islands, Old Ranch Canyon had few natural shelters (e.g., caves, rockshelters). It also lacked high quality chert quarries like those identified on eastern Santa Cruz Island (Arnold 1987; Perry 2004). Only a few low quality chert exposures were found in Old Ranch Canyon, and none were associated with a site. This local chert was used to make expedient tools, which were found at a few sites. However, none of it appears to have been used to make microdrills. Despite the low availability of natural shelters and source materials for making tools, Old Ranch Canyon was heavily used throughout the Holocene. The density of sites (10 sites/km^2) is the highest recorded of the five canyons surveyed on Santa Rosa Island. Furthermore, ethnohistoric data suggest that CA-SRI-85 and -87 are most likely associated with *Qshiwqshiw* (bird droppings), a Chumash village that was located at the canyon mouth (Johnson 1999; Kennett 2005). This village contains the highest number of baptisms (n=120) recorded for any village on Santa Rosa Island, suggesting that occupation of the canyon was relatively substantial.

A unique aspect of the northeast coast that potentially attracted a large number of people to Old Ranch Canyon was the marsh and paleoestuary system located at the mouths of Old Ranch and adjacent Old Ranch House Canyon (Abalone Rocks). Previous work has demonstrated that this system, currently a marsh, was an estuary during the Early and Middle Holocene (Cole and Liu 1994; Anderson 2002; Rick et al. 2005b). Estuaries—calm sheltered embayments that are rich and productive homes to shellfish, finfish, and other animals—were relatively common on the Santa Barbara mainland coast during the Early and Middle Holocene where they were a focus of human settlement (Erlandson 1994). However, the paleoestuary at Old Ranch Canyon is the only estuary currently documented on the Channel Islands (Rick et al. 2005b). Of the 46 sites recorded at Old Ranch Canyon, over half were shell middens and 8 sites (CA-SRI-81, -89, -191, -192, -673, -679, -687, -694) contained estuarine shellfish, including 5 sites around the canyon mouth and 3 on the ridgetops. In addition to these 8 sites, 6 others (SRI-61, -77, -84, -155, -666, and -667) in the adjacent area also contained estuarine shell, bringing the total known sites with estuarine shellfish to 14. Since Old Ranch House Canyon has never been surveyed, other sites probably exist. The presence of both rocky intertidal and estuarine taxa in the shell middens of this area demonstrate that the people who used and occupied Old Ranch Canyon were able to exploit a wider range of shellfish species than most other locations on the Channel Islands (Rick et al. 2005b; Wolff et al. 2007), making this location a valuable source of food. All of the known estuary sites have been ^{14}C dated, producing a detailed chronology for the use and demise of shellfish habitats in the estuary. Sixteen ^{14}C dates from all 14 sites range from 8180 to 5690 cal BP (see Fig. 3; Rick et al. 2005b), suggesting that, like many estuaries on the mainland, this estuary formed as sea levels rose following the last

glacial period and transitioned to a more freshwater system as sea levels stabilized after 6000–5000 cal BP (Cole and Liu 1994; Anderson 2002; Rick et al. 2005b).

While Early and Middle Holocene sites showed heavy use of the estuary, many sites dating between 7000 and 3500 cal BP were found on hilltops or ridgelines (Fig. 3), reflecting greater use of the interior as well as the coast during this period. Old Ranch trends east–west and consequently is closer to the coast than most other canyons (the maximum distance from the coast is about 2 km), suggesting the definitions of interior in this canyon are slightly different from other areas. However, patterns are consistent with other studies that suggest use of island interiors may have been greatest during the Middle Holocene, with perhaps seasonal movement between the coast and interior to exploit plants (Perry 2004, 2005; Kennett and Clifford 2004; Kennett et al. 2007). For example, during the Early Holocene through the early parts of the Late Holocene (ca. 9500 to 2500 BP), Perry (2004, 2005) noted substantial movement of people on eastern Santa Cruz Island between the coast and interior, with people taking advantage of the diverse resources found in inland and coastal habitats. After about 2500 years ago, people appear to have focused much of their settlement on the coast with the establishment of large villages during the late Middle and Late periods (Perry 2004). A survey of the Coches Prietos drainage on the south coast of Santa Cruz Island suggests that people still continued to venture out into smaller, outlying sites, including rockshelters during the Late period (Peterson 1994). This is consistent with the Old Ranch settlement strategy, which, after about AD 500, focused on large village sites situated adjacent to the modern shoreline. However, a small number of sites dated after about 2500 years ago, including two rockshelters, hilltop sites, and other locations on the interior of the canyon indicate that people continued to use these outlying areas throughout the Late Holocene (see also Peterson 1994).

Old Ranch Canyon is adjacent to the most heavily visited public area on Santa Rosa, including the Torrey Pine Grove, Bechers Bay, and campground. This underscores the need for protection, monitoring, and further research in the area. Now that the basic framework of site location, human settlement, and chronology is in place, continued excavation of sites in the area is needed to build a comprehensive trans-Holocene sequence of human cultural developments on Santa Rosa Island. Because just about 40% of Santa Rosa Island has been surveyed (Morris n.d.), it is also clear that additional surveys are needed to identify the scores of unrecorded sites on the island. Ultimately, these surveys are vital for the management and protection of island cultural resources, as well as enhancing knowledge on ancient human occupation of the Channel Islands.

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This project was funded by Channel Islands National Park, the National Park Service Challenge Cost-Share Program, the Western National Parks Association, and Southern Methodist University. I thank Kelly Minas, Ann Huston, and Mark Senning for their help with this research. Todd Braje, Kevin Pemberton, Leslie Reeder, John Robbins, Lauren Willis, and Chris Wolff provided help in the field, and Leslie Reeder and Ameena Tekbali helped compile site records. Tim Coonan, the organizers of the Seventh California Islands Symposium, Lee Lyman, and an anonymous reviewer were instrumental in the production and revision of this manuscript. Finally, I thank Chris Damiani for her keen editorial eye and thoughtful suggestions.

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A PALEOCOASTAL SHELL MIDDEN AT SEAL CAVE (CA-SMI-604), SAN MIGUEL ISLAND, CALIFORNIA

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Abstract—Archaeological test excavations at Seal Cave, a multi-component shell midden located on Harris Point on San Miguel Island, produced evidence for occupation by Paleocoastal peoples between about 10,200 and 9100 calendar years ago. In this paper, we describe the context and chronology of the early archaeological strata at Seal Cave, including faunal remains and artifacts from the Paleocoastal levels. The well-preserved faunal assemblage is dominated by mussels and other rocky shore shellfish, with lesser quantities of marine fish, sea bird, and sea mammal bone. Artifacts recovered include several spire-removed *Olivella* shell beads, a small assemblage of bone tools and tool-making debris, and chipped stone tools made from local Tuqan and Cico cherts. Our results provide valuable information on the nature of maritime Paleocoastal peoples and San Miguel Island ecosystems during the Early Holocene.

INTRODUCTION

The past decade has seen growing interest in the possibility that the peopling of the Americas may have included one or more coastal migrations from northeast Asia (see Erlandson 2002; Erlandson et al. 2007; Fedje et al. 2004; Kemp et al. 2007). Testing this idea is difficult, however, because global sea levels have risen more than 120 m since the end of the last glacial, drowning the late Pleistocene coastlines that early maritime peoples would have followed on such a journey. Despite such problems, California's northern Channel Islands have produced the earliest evidence for seafaring, island colonization, and maritime subsistence in the Americas (see Erlandson 2007; Johnson et al. 2002; Kennett 2005; Rick et al. 2005). More than 40 archaeological sites occupied between about 13,000 and 8000 years ago (cal BP) have been identified on the islands, including four terminal Pleistocene sites dated between about 13,000 and 11,400 years ago and at least three Early Holocene sites occupied roughly 10,000 years ago (Erlandson et al. 2008b). Among the oldest shell middens in North America, these sites provide important information on the antiquity and nature of early maritime cultures along the Pacific Coast. So far, however, few of these early Channel Island sites have been excavated, fully analyzed, and reported. In this paper, we report the results of our recent investigations of a Paleocoastal shell midden in Seal Cave (CA-SMI-604) on San Miguel Island, a rock shelter located on the rugged tip of Harris Point (Fig. 1) that appears to have been first occupied about 10,000 years ago (cal BP). The site adds significantly to the evidence for a substantial settlement of the northern Channel Islands by seafaring Paleocoastal peoples.

A BRIEF HISTORY OF INVESTIGATIONS AT SEAL CAVE

In searching for early archaeological sites on the northern Channel Islands, we focused on geographic features that attracted early islanders inland from now submerged shorelines. These include: (1) caves or rock shelters used for shelter;

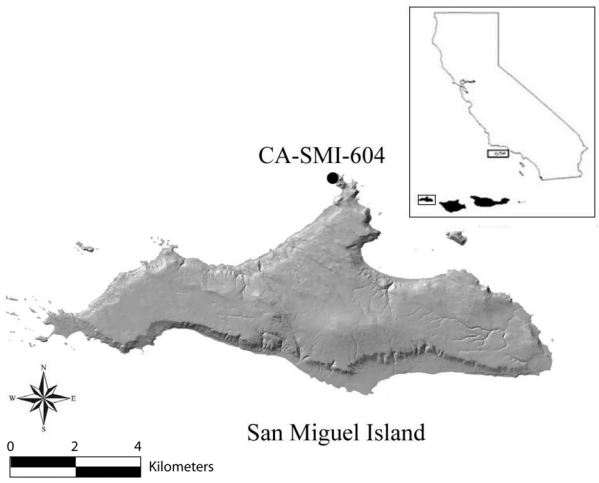

Figure 1. Map of Santa Barbara Channel area showing the general location of Seal Cave (CA-SMI-604).

(2) springs that provided freshwater, especially during the relatively dry summer and fall seasons; and (3) outcrops of chert or other siliceous rocks suitable for making stone tools. Seal Cave was first identified in 2001 by University of Oregon archaeologists assessing the condition of known archaeological sites on San Miguel Island for the National Park Service (Rick and Erlandson 2004). During a visit to two recorded open-air middens near the northwest tip of Harris Point, we noticed a cave prominently positioned at the top of a steep cliff facing westward towards Simonton Cove (Fig. 2). No archaeological site was recorded in this location and no mention of a cave or rock shelter was found in site records for the nearby middens. Climbing up to the cave, we found archaeological materials scattered on the relatively level floor of a rock shelter with an arch-like ceiling over 2 m high. Any archaeological materials that once may have existed on the slope outside the rock shelter had been lost to sea cliff retreat, which is still actively eroding a shell midden deposit along the drip line of the cave. Because two other cave sites on San Miguel contain archaeological deposits of terminal Pleistocene or Early Holocene age, the identification of another cave site was of considerable interest. To establish the depth and age of the midden inside Seal Cave, we excavated a small trowel probe to determine the depth of the deposits and collect radiocarbon (^{14}C) samples for dating. Two ^{14}C dates for well-preserved mussel shells from near the top and bottom of the midden suggested that the site was occupied between about 10,150 and 9200 years ago (Rick et al. 2003). To determine the nature of the archaeological materials being lost to coastal erosion, we returned to the site in 2003 and 2006 to excavate a small test pit and document the site structure, stratigraphy, chronology, and contents.

In keeping with National Park Service policy, our excavations were limited in nature, starting with a small 15 x 20 cm wide trowel probe through about 25 cm of intact midden deposits. We later excavated a 1.0 x 0.5 m test unit roughly in the center of the back wall of the rock shelter. This test pit, designated Unit 1, was excavated in two (50 cm x 50 cm) stages—the southern half (1S) in 2003 and the northern half (1N) in 2006. Each half was excavated in 5 cm levels, with every effort made to remove discrete strata separately. In the southern half of the unit, all excavated sediments were screened over 1/8-inch mesh, with screen residuals transported to the University of Oregon for analysis under controlled lab conditions. Sediments from the northern half of the unit were screened over 1/16-inch mesh in the field, with whole shells, animal bones, and artifacts recovered during field sorting.

In the lab, we cleaned and sorted screen residuals into general categories: chipped stone, shell, bone, or other artifacts; unmodified marine shell, animal bone, charcoal, and uncarbonized plant remains; and non-cultural materials including unmodified rock and other miscellaneous materials. These general categories were analyzed in greater detail, with faunal remains identified to the most specific taxon possible, artifacts described by material and function, etc. All identified materials

Figure 2. Photo of Seal Cave (CA-SMI-604) in 2003, from point to west (photo by J. Erlandson).

were weighed and cataloged, and some materials (e.g., ^{14}C, soil, and isotope samples) were sent off for specialized analyses. In the field and in the lab, the length of whole California mussel (*Mytilus californianus*) shells, which were extremely abundant in the site deposits, were measured as part of a larger study of human impacts on intertidal and near shore ecosystems through the Holocene (Erlandson et al. 2008c). Since the analysis of vertebrate remains from our 2006 excavation has not yet been completed, only a partial account of the faunal assemblage is presented here.

The chronology of the archaeological strata at Seal Cave is based primarily on ^{14}C dating of individual, well-preserved marine shells, correlated with the stratigraphy and temporally diagnostic artifacts recovered or observed at the site. The radiocarbon chronology relies on a combination of two conventional and three AMS (accelerator mass spectrometry) dates, the latter including two dates on small fragments of spire-removed *Olivella* shell beads.

SITE SETTING, SOILS, AND STRATIGRAPHY

The northwest tip of Harris Point is a rugged and remote stretch of San Miguel Island's north-central coast. Seal Cave is located roughly 20 m (~66 feet) above sea level on a sheer cliff overlooking Secret Cove. With an opening facing to the southwest, the cave offers an expansive view of Simonton Cove, Otter Point, and the northwest coast of the island. The coastline in the immediate vicinity is dominated by rocky intertidal habitats, with extensive sand beaches to the south and west in Simonton Cove. Off Harris Point, the ocean bottom plunges rapidly into relatively deep water, so the 26 m isobath that approximates the 10,000-year-old shoreline is less than 200 m from the modern shoreline (Fig. 3).

Seal Cave is a small rock shelter, with a nearly level interior floor about 5 m wide and 3.5 m deep. With a ceiling ranging from about 1.6 m to 2.7 m high, the central part of the shelter offers ample headroom for people to stand in the interior. Midden deposits cover the entire floor and probably once draped the slope outside the shelter. On this cave floor we found a dark grayish-brown anthropogenic soil strewn with marine shells, animal bones, bird feathers, occasional artifacts, and some plant remains. Artifacts noted on the surface included several spire-removed *Olivella* beads, a small shell disk bead, a fragment of a circular shell fishhook, and a few pieces of chert tool-making debris. Also found on the surface was evidence for animal (probably seabird) activity and two human bones. The human bones, apparently from a single individual buried in the northeast corner of the cave, were left in place and no excavations were conducted in this area.

Along with erosion along the southern edge of the rock shelter, some evidence for disturbance of the floor was evident, potentially caused by both humans and animals. The presence of the human bones on the site surface suggested some erosion or disturbance of the site deposits, although no looters' pits or other signs of previous excavation were apparent. Sheep disturbed some Channel Island caves after their introduction in the mid-1850s, and may have caused erosion to the upper portion of the midden deposits. Cormorants and possibly other birds have also nested or roosted in the cave, depositing some animal bones, plant remains, feathers, guano, and other organic debris.

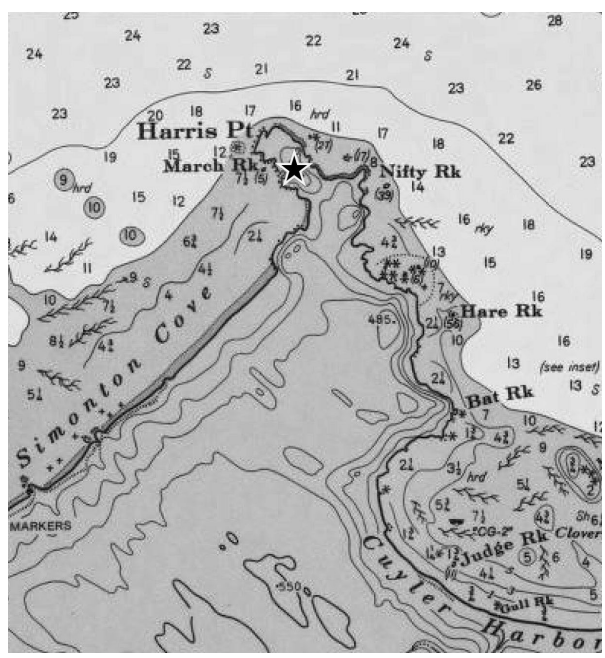

Figure 3. Topography and bathymetry of the Harris Point area, showing the 10 fathom (18 m) isobath, approximating the Early Holocene shoreline in the Seal Cave (marked by star) vicinity (soundings in fathoms, from NOAA 1987 navigation chart for San Miguel Passage).

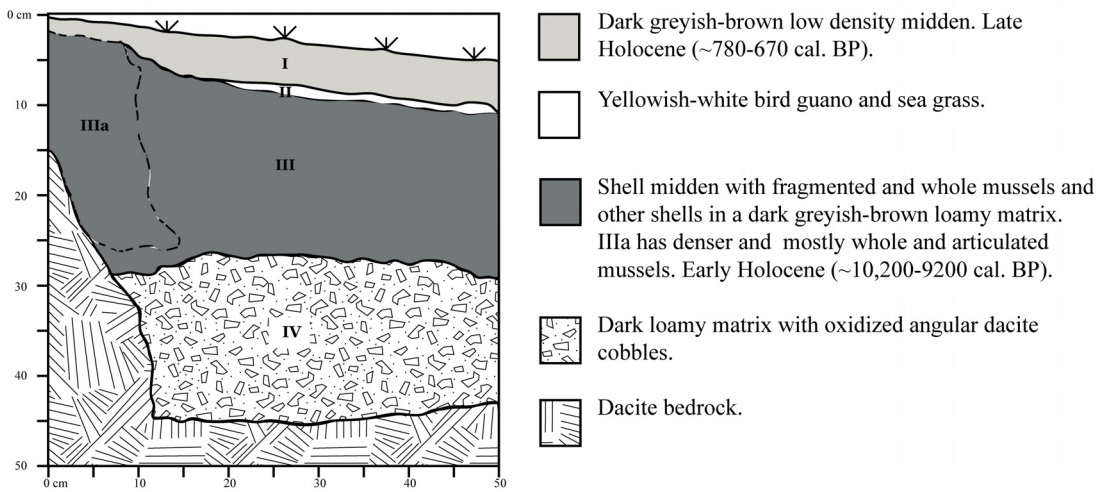

Figure 4. Stratigraphic profile of the south wall of Unit 1S at Seal Cave (CA-SMI-604). Drafted by T. Davis from original field drawing by J. Erlandson.

We also identified clear evidence for stratigraphic integrity in the remaining midden deposits. In Unit 1, for instance, we identified a thin (<1 cm thick) and discontinuous yellowish-white stratum (II) 4–6 cm below the surface that separated shell midden deposits (Strata I and III) above and below it—marking what appeared to be a break in the cave occupation (Fig. 4). During excavations, we also found numerous articulated mussel shells (Stratum IIIa)—especially near the walls of the cave in the Early Holocene layers. The outstanding preservation of faunal remains—including remnants of periostracum on some very old mussel shells—suggests that portions of the midden deposits were buried relatively quickly and were not disturbed or exposed again until our excavations.

Below the archaeological deposits, we found a dark and very loose soil (Stratum IV), densely studded with small angular cobbles. We encountered occasional voids while excavating this basal soil, but it did not appear to contain archaeological materials. Due to time limitations we were never able to penetrate more than about 10–15 cm into this dark soil and its origin is not well understood. The source of the angular cobbles seems likely to have been the weathering of the dacite bedrock of the cave walls, and the dark color of the soil could result, in part, from the percolation of fine organics downward from the overlying midden.

ANALYTICAL RESULTS

Chronology

Five ^{14}C dates are available for marine shell samples from Seal Cave (Table 1). The first of these was a date of 9440 ± 50 RYBP (OS-34804), with a calibrated age range of 10,140–9940 cal BP, obtained for a well-preserved California mussel shell recovered from near the base of a small probe excavated into the midden in the north end of the shelter floor. After excavating the 50 x 50 cm wide Unit 1S, we obtained two additional dates of 1340 ± 60 RYBP (Beta-181393; 780–670 cal BP) and 9030 ± 90 RYBP (Beta-171120; 9470–9175 cal BP) for unmodified shells from the 0–5 cm and 5–10 cm levels, respectively. The younger date confirmed a suspected Late Holocene occupation of the site indicated by the grooved shank fragment from a circular or j-shaped shell fishhook and a small shell disk bead found on the site surface.

The older date from the 5–10 cm level suggests that the bulk of the midden deposit (~5–30 cm) dated to the very Early Holocene. Two additional dates were later obtained for small fragments of two spire-removed *Olivella biplicata* shell beads, which have been found in several Early Holocene sites on the northern Channel Islands (see Morris and Erlandson 1993; Erlandson et al. 2005). Unexpectedly, these beads were dated to 6875 ± 25 RYBP (UCIAMS-8676; 7240–7150 cal BP) and

Table 1. ^{14}C dates for marine shells from Seal Cave (CA-SMI-604).

Sample provenience	Lab no.	Material	^{14}C age	Calendar age (cal BP)
Unit 1S: 0–5 cm	Beta-181393	CA mussel	1340 ± 60	780–670
Unit 1S: 5–10 cm	UCIAMS-8676	*Olivella* bead	6875 ± 25	7240–7150
Surface: sea cliff area	UCIAMS-8675	*Olivella* bead	6960 ± 25	7320–7220
Unit 1S: 5–10 cm	Beta-171120	CA mussel	9030 ± 90	9470–9175
Probe: ~25 cm (midden base)	OS-34804	CA mussel	9440 ± 50	10,140–9940

Notes: Calendar age ranges BP (before "present" = AD 1950) at one sigma. Calibrated using CALIB 5.01 with a Δ R of 225 ± 35.

6960 RYBP (UCIAMS-8675; 7320–7220 cal BP), suggesting that CA-SMI-604 was also utilized about 7200 years ago. Because no midden refuse has been dated to this time period, these beads may be associated with a ritual use of the cave, deposited along with the human bones exposed on the site surface.

Artifacts

Given the limited nature of our excavations and the loss of refuse areas outside the cave to coastal erosion, the number of artifacts recovered from the Paleocoastal levels of Seal Cave is relatively small. They include a small assemblage of chipped stone artifacts dominated by tool-making debris, two crude biface fragments, and a few expedient tools; a few *Olivella* shell beads and bone artifacts; and several pieces of bitumen (asphaltum) probably used as a glue or sealant. The bitumen was found all the way to the base of the Paleocoastal midden and is probably derived from a large oil seep located off the northwest coast of San Miguel Island.

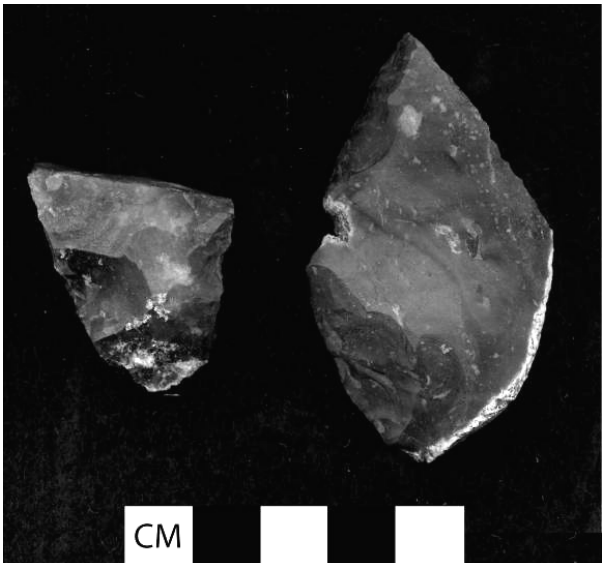

Figure 5. Two crude bifaces from the Paleocoastal levels at Seal Cave, both made from Tuqan Monterey chert (scanned image by T. Davis).

The chipped stone artifacts recovered from Unit 1 consist primarily of tool-making debris made of Tuqan and Cico cherts. Once thought to have been imported from the mainland, these rock types are now known to be available in geological outcrops near the east end of San Miguel (Erlandson et al. 2008a). Two crude bifaces made from Tuqan Monterey chert were also recovered from the Paleocoastal levels of Unit 1 (Fig. 5), one broad and roughly leaf-shaped specimen made from a large flake removed from a Tuqan chert cobble, and one fragment that appears to have broken during the early stages of manufacture.

Of the eight shell beads recovered from Seal Cave, seven are spire-removed *Olivella biplicata* beads which are found in Early Holocene and later sites in the Santa Barbara Channel area (King 1990). As noted above, two of these beads were directly dated to about 7200 calendar years ago. The other *Olivella* beads could be of similar age, but some may be associated with the Early Holocene occupation. A single shell disk bead found on the site surface was heavily weathered and could not be identified to a specific taxon or bead type. The only other shell artifact found at Seal Cave was a grooved shank fragment from a circular or j-shaped fishhook observed on the site surface in 2001. Although not collected, this fishhook fragment is almost certainly associated with a Late Holocene occupation of the cave.

Also recovered from the Paleocoastal levels were two bone tools (Fig. 6). The first is a bird bone

Figure 6. Bird bone tools and tool-making debris from Paleocoastal levels at Seal Cave (left to right: 604-204 bone splinter; 604-112, gorge preform with cut longitudinal groove; 604-111, bone splinter; 604-141, ground awl-like tool sawn off at base; scanned image by T. Davis).

awl or pin, cut and squared off on one end and sharpened to a point on the other. The second appears to be an unfinished bone gorge, partially ground to a point on both ends. On the interior surface of the bone, a groove was carefully cut or sawn along the long axis of the gorge. This pattern is consistent with a "saw-and-snap" technique documented for the manufacture of bone gorges in the Early Holocene levels at Daisy Cave (Rick et al. 2001). Several shattered fragments of bird bone recovered may also represent debris from gorge or other bone tool making.

Faunal Remains

The faunal assemblage from Seal Cave is comprised primarily of the remains of marine shellfish, including over 15 kg of shell recovered from the Paleocoastal levels of Unit 1S (Table 2). At least 24 separate shellfish taxa are represented in this sample, with a minimum number of 3368 individual (MNI) organisms, almost exclusively from rocky intertidal habitats. Many of these shellfish taxa provide only miniscule proportions of the assemblage by weight, however, and appear to be either minor dietary contributors (e.g., *Tegula*, crabs, and chitons) or incidental additions to the midden (tiny limpets, barnacles, and gastropods, etc.). The assemblage is dominated by mussels (especially sea mussels, *Mytilus californianus*) which comprise almost 92% of the total weight of shell recovered from the Paleocoastal levels and over 74% of the MNI. In contrast, among the other shellfish species intentionally harvested by Paleocoastal peoples, owl limpets (*Lottia gigantea*) contribute only about 1.2% of the shell weight (MNI = 34, <1% of the total), while black and red abalones (*Haliotis cracherodii* and *H. rufescens*) together comprise only about 1.0% of the shell weight and only 12 individuals. Although they provide only about 1.6% of the shell by weight, leaf or gooseneck barnacles (*Pollicipes polymerus*) are relatively abundant compared to most San Miguel Island shell middens.

The abundance of very small mussels in the assemblage suggests that mussels were stripped off intertidal rocks in clumps or mats. The abundance of articulated mussels in the Seal Cave midden also indicates that mussels were carried to the site whole, where they were processed and discarded after consumption. Such a harvesting and processing pattern probably introduced numerous epifauna into the midden, including the scores of very small barnacle, limpet, and gastropod shells found in the sample from Seal Cave. Aggregations of leaf barnacles often live among mats of California mussels and platform mussels (*Septifer bifurcatus*), so these edible barnacles may have been harvested simultaneously as clumps of mussels were stripped from intertidal rocks. Such stripping techniques may also help explain the relatively small average size of California mussels in the Paleocoastal strata. The mean size of 363 whole California mussel shells from the 5–25 cm levels was just 36.8 mm, the lowest value yet recorded for a site older than 8000 years (Fig. 7; see Erlandson et al. 2008c). The mean size of the mussels also declines from the Early Holocene to Late Holocene, with 32 whole shells from the 0–5 cm level averaging just 25.3 mm long.

The vertebrate remains from Seal Cave have not yet been fully analyzed, but the Paleocoastal levels produced small amounts of marine fish, bird, and mammal bone. The low density of vertebrate remains is typical of most Early Holocene sites (other than Daisy Cave) on the northern Channel Islands and the adjacent mainland (see Erlandson 1994). Most of the fish remains consist of unidentifiable bone fragments, but among the identifiable elements analyzed so far, surfperch (Embiotocidae), California sheephead (*Semicossyphus pulcher*), senorita (*Oxyjulis*

Table 2. Shellfish remains from the Paleocoastal levels of Unit 1S at Seal Cave (CA-SMI-604).

	5–10cm		10–15cm		15–20cm		20–25cm		25–30cm		Total	%	Total	%
Taxon	MNI	Wt.	MNI	Wt.	MNI	Wt.	MNI	Wt.	MNI	Wt.	MNI	MNI	Wt.	Wt.
Acanthina punctulati							1	0.1			1	-	0.1	-
Amphissa columbiana	1	0.1					1	0.1			2	0.1	0.2	-
Balanus spp.	130	159	96	127	46	44.6	27	22.4	1	1.1	300	8.9	354.8	2.4
Chiton, undif.	1	0.5	2	5.1	1	3.6	1	1.8			5	0.2	11.0	0.1
Clam, undif.	2	0.2	2	0.2						0.5	4	0.1	0.9	-
Crab, undif.	1	1.1		1.5	1	5.8	1	6.0			3	0.1	14.4	0.1
Crepidula adunca							1	0.1			1	-	0.1	-
Fissurella volcano	1	0.3	2	1.4					1	0.1	4	0.1	1.8	-
Gastropods, undif.	12	0.9	9	0.3	7	0.3	2	0.1			30	0.9	1.6	-
Haliotis cracherodii	2	23.4	5	66.5	3	20.7					10	0.3	110.5	0.7
Haliotis rufescens		2.6									0	-	2.6	-
Haliotis, undif.	1	14.6		11.5				6.3	1	17.7	2	0.1	50.1	0.3
Lacuna vincta			4	0.4			1	<0.1			5	0.2	0.4	-
Limpet, undif.	149	10.8	168	16.1	92	6.4	78	18.4	3	0.2	490	14.6	51.8	0.3
Littorina planaxis			2	0.4			1	0.06			3	0.1	0.4	-
Lottia gigantea	14	49.8	15	92.3	5	30.3				1.1	34	1.0	173.5	1.2
Modiolus modiolus	2	0.4	2	0.5	1	0.2					5	0.2	1.2	-
Mytilus californianus	324	3759	924	6102	479	2659	215	1011	43	120	1985	59.1	13652	90.6
Olivella biplicata	1	0.4			1	<0.1	1	0.4			3	0.1	0.9	-
Pollicipes polymerus	1	113	1	59.7	1	38.8	1	22.4	1	0.8	5	0.2	234.2	1.6
Septifer bifurcatus	18	10	150	60.1	152	61.2	102	32	18	5.1	440	13.1	168.3	1.1
Serpulorbis spp.	1	1.3	1	1.0	1	1.7					3	0.1	4.0	-
Shell, undif.		83.9		47.6		3.1		2328		0. 7	0	-	158. 7	1.1
Strongylocentrotus spp.	1	13.3	1	16	1	4.2	1	2.4	1	0.1	5	0.2	36.0	0.2
Tegula brunnea	1	0.3									1	-	0.3	-
Tegula funebralis	4	4.1	5	11.8	5	15.6	1	7.8		0.4	15	0.4	39.7	0.3
Thais canaliculata	3	0.1	1	0.3					1	0.5	5	0.2	0.9	-
Thais spp.	3	1.7	1	0.4	3	1.9			1	0.4	8	0.2	4.4	-
Totals	673	4251	1391	6622	798	2897	435	1155	71	149	3368	100.0	15074	100

Note: Based on 1/8-inch screen recovery; MNI = minimum number of individuals.

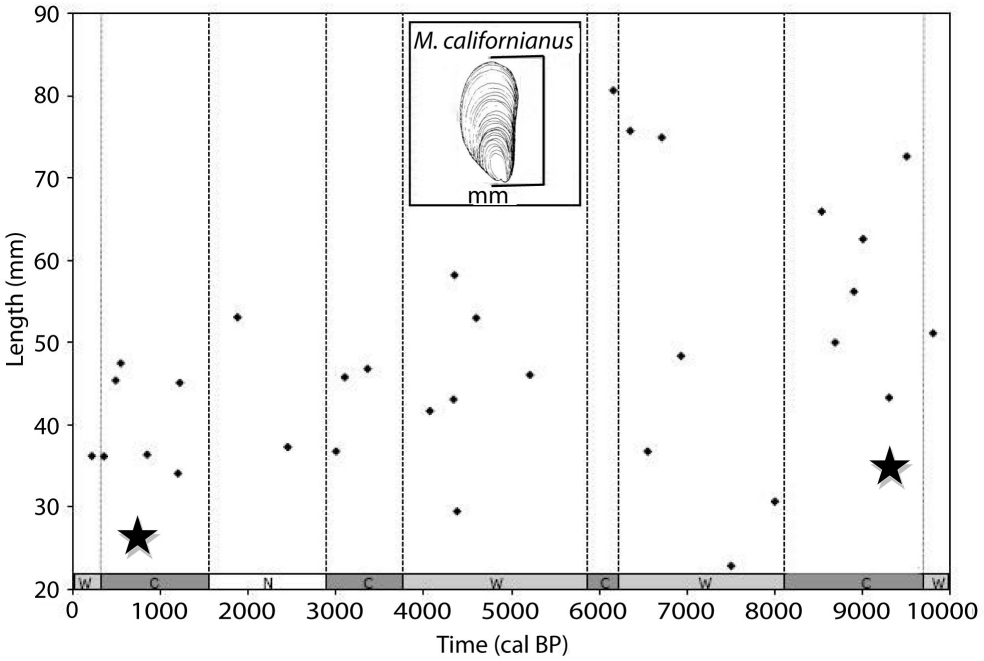

Figure 7. Mean California mussel shell size in Early and Late Holocene components (marked by black stars) at Seal Cave, compared to other San Miguel Island sites (adapted from Erlandson et al. 2008c). The bar at the base identifies periods of relatively cool (c), warm (w), or intermediate (n) sea surface temperatures (see Kennett 2005).

californica), ling cod (*Ophiodon elongatus*), rockfish (*Sebastes* spp.), and hound shark (Triakidae) have been identified. All these fish taxa can be caught in kelp forest and other near shore habitats off San Miguel Island. The large mammal remains recovered are fragmented and mostly unidentifiable, but at least some appear to be from sea mammals.

SUMMARY AND CONCLUSIONS

Although limited in scope, our research at Seal Cave has produced valuable information on the antiquity and nature of early maritime adaptations on San Miguel Island. Much of the site appears to have been lost to coastal erosion, but data recovered from the site remnants suggest that the cave was used episodically by the Chumash and their predecessors during the Early, Middle, and Late Holocene. The most recent of these episodes was an occupation about 700 years ago (AD 1250), represented by the truncated midden remnants found in the upper 4–6 cm of Unit 1. A Middle Holocene use of the cave, presently identified only by AMS ^{14}C dates for two *Olivella* beads of about 7200 years ago, may be related to a ritual use of the rock shelter as a burial place. The most extensive use of the cave is marked by 20–25 cm of dark anthropogenic midden soil deposited between about 10,150 and 9200 years ago, possibly during two or more discrete occupations by Paleocoastal peoples. While it seems likely that the early occupation of the cave was intermittent, the lack of microstratigraphy and the available ^{14}C dates do not currently allow further resolution of the early occupational chronology.

Due to the small size of the artifact assemblage and the lack of detailed data on the vertebrate remains, the conclusions we can make about the nature of Paleocoastal adaptations at Seal Cave are limited. Nonetheless, several aspects of the assemblage are generally consistent with data from several other Early Holocene sites on San Miguel Island, including: (1) a heavy economic emphasis on shellfish collecting in rocky intertidal habitats; (2) faunal and artifactual evidence for a broader subsistence economy that included marine fishing and hunting; (3) an early fishing technology that employed bone gorge fishhooks carefully manufactured with a combination of "saw-and-snap" and grinding methods; (4) a chipped stone

technology including bifaces and expedient tools made primarily from local raw material types, including Tuqan and Cico cherts, as well as coarse-grained metavolcanic cobbles; and (5) spire-removed *Olivella* beads used for personal ornamentation.

Because Seal Cave is rapidly being lost to coastal erosion, we are fortunate to have identified the Paleocoastal and later components at the site before they were completely destroyed. Seal Cave is one of over 30 archaeological sites on San Miguel Island now known to have been occupied on one or more occasions between about 12,000 and 8000 years ago. As such, it provides additional evidence for a relatively substantial presence of early maritime peoples on the northern Channel Islands. The antiquity and number of early sites is particularly impressive considering that the shorelines and extensive coastal lowlands of the terminal Pleistocene and Early Holocene have been lost to erosion or submerged by rising seas since the Last Glacial Maximum. Given the number and variety of early sites documented in the area, however, it seems increasingly likely that there was a permanent occupation of the northern Channel Islands by Paleocoastal peoples, beginning as much as 13,000 years ago. Whether these early Channel Islanders were descended from maritime people who followed the coastlines from Asia into the Americas is not yet known. What is clear is that the Channel Islands and the Pacific Coast of North America were settled by relatively sophisticated maritime peoples much earlier than most American archaeologists would have believed possible just a decade or two ago.

ACKNOWLEDGMENTS

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ANCIENT SEA MAMMAL EXPLOITATION ON THE SOUTH COAST OF SAN MIGUEL ISLAND

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Abstract—Archaeological evidence suggests that pinnipeds and sea otters have long been important dietary and raw material resources for Channel Islanders. Excavations at a village site on the south coast of San Miguel Island, CA-SMI-232, provide evidence of sea mammal hunting at about 1200 cal BP. Detailed analysis demonstrates that Guadalupe fur seals were the focus of Late Holocene hunters, with lesser numbers of California sea lions, harbor seals, and sea otters. Since federal protection and the subsequent rebound in populations after historic over-hunting, tens of thousands of pinnipeds haul out each year on San Miguel Island beaches and rocky outcrops. Today, breeding populations are dominated by northern elephant seals, California sea lions, northern fur seals, and harbor seals with occasional visits by Steller's sea lion and Guadalupe fur seals. The archaeological record suggests a complex picture of local pinniped population dynamics that has been severely altered by historic exploitation, and perhaps by large-scale prehistoric hunting. In this paper, we present zooarchaeological evidence of pinniped hunting from CA-SMI-232 and document significant changes between prehistoric and modern pinniped communities on San Miguel Island.

INTRODUCTION

Beginning in the eighteenth and nineteenth centuries, commercial hunting substantially reduced Pacific Coast populations of seals (family Phocidae) and sea lions (family Otariidae). History is replete with stories of commercial hunting ships from Russia, Britain, America, and elsewhere slaughtering hundreds to thousands of sea mammals at a time for voracious consumer markets. Along with well-documented impacts on whale populations, some of the most dramatic examples may be the hunting of sea otters (*Enhydra lutris*), Guadalupe fur seals (*Arctocephalus townsendii*), northern fur seals (*Callorhinus ursinus*), California sea lions (*Zalophus californianus*), elephant seals (*Mirounga angustirostris*), and others in the New World. European and American commercial interests discovered vast populations of sea mammals from Alaska south to the Antarctic and frantically competed for animal skins and oil (Ellis 2003, 161–178). Despite surviving millennia of predation by Aleut, Chumash, and other Native hunters, many sea mammal species were brought to the brink of extinction within a few decades of commercial hunting.

Since the passing of the Marine Mammal Protection Act of 1972, pinniped and sea mammal populations have made a dramatic recovery despite significant historic population size reductions (population bottlenecks) and in some cases, decreases in genetic variability (genetic bottlenecks). Today, the Channel Islands are home to abundant pinniped and cetacean (dolphins, whales, etc.) populations. Point Bennett, located at the west end of San Miguel Island, is one of the largest and most diverse pinniped rookeries in the world occupied by over 150,000 animals yearly (DeLong and Melin 2000). Six different pinniped species regularly visit the island with breeding populations dominated by northern elephant seals, California sea lions, northern fur seals, and harbor seals (*Phoca vitulina*) with occasional visits by Steller's sea lion (*Eumetopias jubatus*) and Guadalupe fur seals. Sea otters were reintroduced to San Nicolas Island but have not been allowed to establish populations at other islands in an effort to reduce impacts by this voracious shellfish predator

on sea urchin and other fisheries in areas south of Point Conception.

In this paper, we present zooarchaeological evidence of pinniped hunting from CA-SMI-232, a large Late Holocene village site on the south coast of San Miguel Island, and use these data and other archaeological assemblages to compare against the modern composition of sea mammals. We argue that modern communities of pinnipeds are a product of severe historic over-hunting, their subsequent protection, and the recovery of seal and sea lion populations in a demographic vacuum. The large, diverse rookery on western San Miguel Island has probably not existed for a large part of the last 13,000 years following the initial colonization of the northern Channel Islands by maritime peoples.

ENVIRONMENTAL AND CULTURAL CONTEXT

San Miguel Island is located approximately 42 km off the Santa Barbara Coast, and the 37 km^2 island is comprised of rolling hills, sprawling dune sheets, tablelands, and marine terraces (Schoenherr et al. 1999). Terrestrial habitats on the island are relatively impoverished, lacking many of the plants and animals common on the mainland. However, a rich and ecologically diverse marine environment surrounds the island, with strong deep-water upwelling and nutrient-rich kelp forests supporting sizeable populations of shellfish, fish, sea mammals, and seabirds.

At historic contact, these extensive marine resources supported dense populations of maritime hunter-gatherers, the Chumash Indians. Spanish chroniclers described large villages and towns, led by hereditary chiefs scattered along the mainland coast and island perimeters. Goods and services were regularly traded between the islands, mainland, and interior with purple olive snail (*Olivella biplicata*) beads serving as the medium of exchange (Arnold 1991, 1992, 2001; Kennett 2005; King 1990; Rick 2007; Rick et al. 2005).

Scientific archaeological investigations have been conducted on San Miguel and the other Channel Islands for over a century and have yielded a dynamic picture of island subsistence strategies. While considerable temporal and spatial variation has been identified, islanders seem to have focused on intertidal shellfish gathering during the Early Holocene. Less accessible resources such as fish, sea mammals, and seabirds gradually contributed a greater percentage of the dietary meat, as

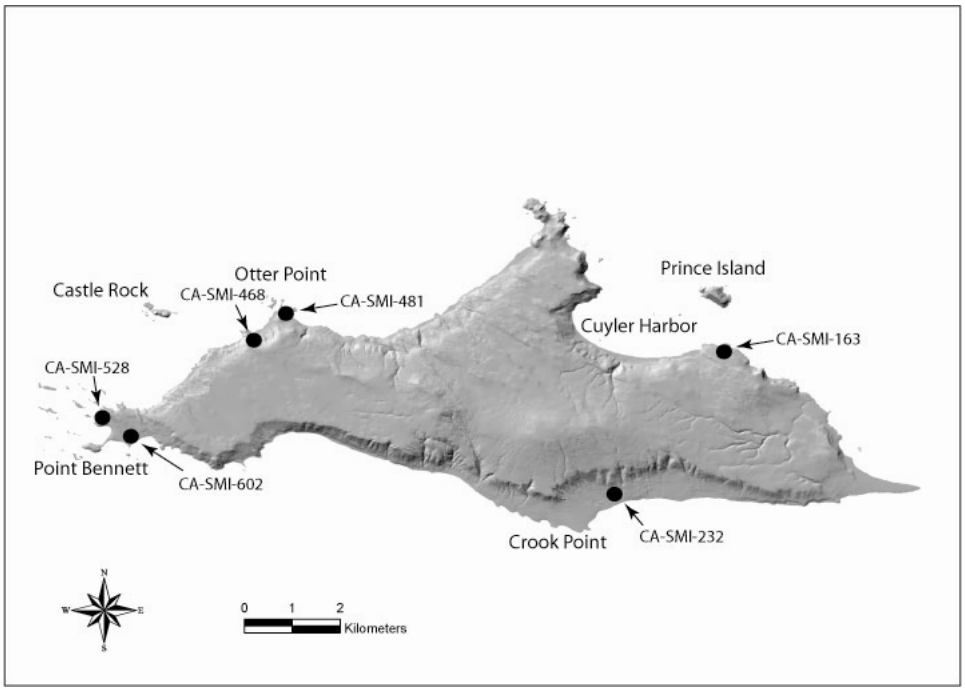

Figure 1. Location of San Miguel Island, the Santa Barbara Channel region, and the archaeological sites mentioned in the text.

populations expanded and anthropogenic impacts affected the availability of local resources (Braje 2007; Braje et al. 2007; Erlandson 1994; Kennett 2005; Rick 2007; Rick et al. 2005). Pinniped hunting experienced an abrupt increase beginning about 1500 cal BP (Braje 2007; Kennett 2005; Rick 2007; Walker et al. 2002). Three sites on San Miguel Island dating to this time period have undergone archaeological sampling and detailed faunal analysis, and contain abundant pinniped remains—CA-SMI-481 at Otter Point (Rick 2007), CA-SMI-528 at Pt. Bennett (Kennett 2005; Walker et al. 2002), and CA-SMI-232 on the south-central coast (Braje 2007). In the following section, we present zooarchaeological data on marine mammal remains from excavations at CA-SMI-232. Our analysis provides a broader understanding of the nature of sea mammals available to San Miguel islanders during the Late Holocene, the technological and economic context of sea mammal hunting, and the impacts of growing populations on marine ecosystems.

METHODS

CA-SMI-232 is a large shell midden positioned on the south coast of San Miguel Island, near the base of the southern escarpment, northeast of Crook Point (Fig. 1). The site was first recorded in the 1960s by Rozaire and Kritzman (Rozaire 1978), who mismapped the locality approximately one km to the east. During an archaeological survey project of the south coast, Braje and colleagues relocated, mapped, and described the locality (Braje et al. 2005). The site has a commanding view of the Crook Point area and its relatively protected harbor, sandy beaches, dense offshore kelp forests, and the southern coastal plain. The site deposits are exposed in two actively eroding gullies approximately 150 m west of Forney's Canyon, a large canyon with seasonal freshwater (Fig. 2).

The West Gully contains a 20 to 30 cm thick shell midden deposit, abundant in rocky shore shellfish remains, especially mussel, small red and black abalone, and sea urchin shells. This deposit is exposed for approximately 50 m in the eastern wall and, while not continuous, the midden seems to represent a single occupation based on the similar stratigraphic location and cultural constituents of the deposits. The East Gully contains midden deposits between 30 and 60 cm thick and relatively continuous intact deposits are exposed for roughly 80 m in its eastern and western walls. Deposits are notable for their size, thickness, and density and all contain abundant shellfish, fish, and marine mammal remains. Visual inspection of the deposits, however, suggests that two distinct types of deposits are eroding from this gully. In the northeast site area, the midden exposed in the western wall is dominated by shellfish remains; fish and marine mammal bone are present but significantly less abundant than shell. Two pockets of midden dominated by marine mammal bones are also present—one approximately 10 m south of the shell lens in the western wall and one opposite the shell lens eroding from the eastern wall. These "bone bed" loci contain dense aggregations of articulated and disarticulated skeletal remains of fish and sea mammal, including many juvenile pinnipeds and some cetacean remains.

Research at CA-SMI-232 focused on the shell and bone lenses exposed in the East Gully exposure, but radiocarbon samples were collected from the midden deposit in the West Gully. Two columns, a 75 L sample from the bone bed lens (Column 1) and a 100 L sample from the shell lens (Column 2), were excavated from the gully wall exposures and water-screened over 1/16-inch mesh (Fig. 2). In addition, a 2.0 m by 1.0 m excavation unit (Unit 1) was excavated through the bone bed lens with the long axis running east-west, perpendicular to the gully.

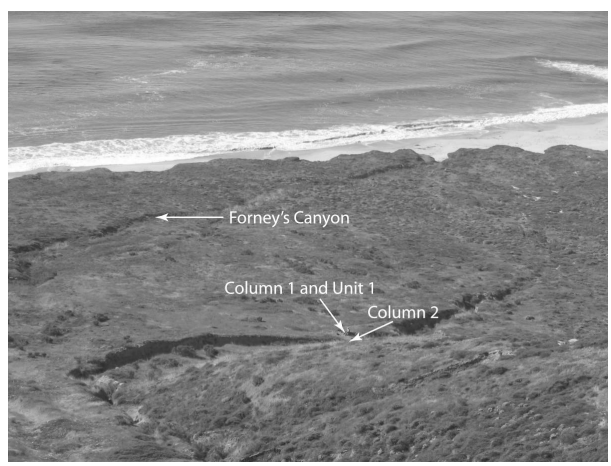

Figure 2. Photograph of the East Gully at CA-SMI-232 and locations of excavation units.

To quantify the various sea mammal remains, a variety of zooarchaeological measures were used, including number of identified specimens (NISP), minimum number of individuals (MNI), and bone weights. NISP is the count of whole and fragmentary elements for each individual taxon. MNI values are an estimate of the lowest possible number of individuals present in the assemblage and are derived from the frequency of non-repetitive elements. While each of these methods has associated problems, taken together they offer an excellent measure of the relative importance of faunal classes.

Excavated samples produced numerous complete or nearly complete sea mammal elements, but many of these were vertebrae and flipper elements that are difficult to positively identify to species. We identified marine mammal bone to the most specific taxon possible, but limited our analysis to elements for which we had access to large comparative collections (e.g., humeri, femurs, mandibles, maxilla, and cranial elements) or those that are distinctive to family, genus, or species (e.g., cetacean vertebrae). Due to these limitations, the three excavated samples are reported as a single assemblage. The ages and sexes of the pinniped bones were determined using the research osteological collection at the National Marine Mammal Laboratory in Seattle. Sea otter bones were excluded from this analysis because of the small sample size and limited sexual dimorphism in the skeletal remains.

RESULTS

Four radiocarbon dates define the site chronology (Table 1). From the East Gully exposures, three radiocarbon dates were obtained from single, well-preserved marine shells, one from the top of the bone lens, one from the top of the shell lens, and one from the base of the shell lens. These dates suggest that the East Gully midden was deposited between about 1290 and 1070 cal BP. Since stratigraphic profiles show no evidence of a hiatus in the cultural strata, these deposits probably date to a relatively narrow window of time and reflect discrete activity areas.

A single radiocarbon sample was run from the West Gully shell midden deposit—an *Olivella* wall bead collected from the middle of the shell deposit in the eastern wall, yielding a one sigma age range of 600 to 490 cal BP. This suggests that the area was occupied at least 500 years after the East Gully occupation. Surface collections from the West Gully produced several *Olivella* callus cup beads, a hallmark of the Late Period and consistent with the radiocarbon chronology (see King 1990). No diagnostic Late Period artifacts were found in the East Gully site area, suggesting that the material corresponds with the end of King's (1990) Middle Period.

Based on the two column samples (total = 175 L), sea mammal bone density at CA-SMI-232 was extremely high at 32.7 g/L, often less than 10 g/L at other Late Holocene sites (see Braje 2007; Rick

Table 1. Radiocarbon dates from CA-SMI-232.

Provenience	Material[1]	Lab #	Measured ^{14}C age	Conventional ^{14}C age	Age range (cal BP)[2]
East Gully, Column 1, level 1	*Mc*	OS-44639	N/A	1910±30	1290-1190
East Gully, Column 2, level 1	*Ol*	OS-59576	N/A	1880±30	1265-1170
East Gully shell lens, near base	*Hr*	Beta-180770	1370±60	1810±60	1220-1070
West Gully wall, near base	*Ol* wall	OS-51542	N/A	1160±40	600-490

[1]*Hr*=*Haliotis rufescens*, *Mc*=*Mytilus californianus*, *Ol*=partial *Olivella* cup bead, *Ol* wall=*Olivella* wall bead.

[2]Calibrated using the CALIB 5.0.1 program and a local reservoir correction of –225 ± 35 years (Stuiver and Reimer 1993, 1999); age ranges at one sigma.

Table 2. Identified marine mammal remains from Columns 1 and 2 and Unit 1 at CA-SMI-232.

	Wt. (g)	Wt.%	NISP	NISP%	MNI	MNI%
Carnivora						
Otariidae						
Arctocephalus townsendii (Guadalupe fur seal)	3518.4	82.6	84	84.8	35	85.4
Zalophus californianus (California sea lion)	537.1	12.6	5	5.1	2	4.9
Phocidae						
Phoca vitulina (Harbor seal)	18.5	0.4	2	2	1	2.4
Mustelidae						
Enhydra lutris (Sea otter)	25.5	0.6	2	2	2	4.9
Cetacea						
Small/Medium Cetacean	162.5	3.8	6	6.1	1	2.4
Total	4262	100	99	100	41	100

2007). Table 2 shows that most of the identified sea mammal remains were from otariids (89.9% of NISP), including 84 from Guadalupe fur seals (84.8%) and five from California sea lions (5.1%). Phocids and sea otter bones were relatively rare in the samples, with only two harbor seal bones (2.0%) and two sea otter bones (2.0%). Six small to medium cetacean bones were identified—probably dolphin or porpoise bones—comprising 6.1% of the total NISP. MNI values reflect similar patterns (Table 2), with otariids comprising 90.3% of the total MNI, phocids 4.8%, and sea otters 4.9%. Guadalupe fur seal was the most abundant marine mammal by MNI, comprising 85.4%, followed by California sea lions and sea otters each at 4.9%. Harbor seals and small and medium cetaceans each accounted for 4.8% of the sample.

Of the 84 Guadalupe fur seal elements identified by age and sex, most (n=49) were adult females. Two were from adult males, three from subadult females, and two from subadult males (Table 3). Sex determinations could not be made on 26 elements due to a lack of comparative collections or sexually dimorphic characteristics. The two identified harbor seal elements were from a pup, which could not be sexed. Finally, five California sea lion bones were identified, four adult males and one subadult male (Table 3). In total, the assemblage is dominated by adult or subadult Guadalupe fur seals with only eight of the identified

Table 3. Age and sex determinations of pinniped bones at CA-SMI-232 identified to species (NISP)

Species	Adult	Subadult	Juvenile	Pup	Male	Female	Sex Undif.
Guadalupe fur seal	53	9	16	6	5	53	26
Harbor seal	--	--	--	2	--	--	2
California sea lion	4	1	--	--	5	--	--

elements from pups, six from Guadalupe fur seals, and two from harbor seals. These pup elements consisted of four humeri, two femurs, one tibia, and one mandible.

DISCUSSION AND CONCLUSIONS

The late Middle Period (ca. 1300–800 cal BP) seems to be a time when Channel Islanders underwent remarkable social, political, economic, and physiological changes. Data suggest that islanders congregated in large coastal villages, increased the production and trade of goods between the islands and mainland, and diversified their subsistence economies (Arnold 2000, 2001; Kennett 2005; Rick 2007; Rick et al. 2005). This also seems to be a time when islanders underwent remarkable declines in human health and increases in disease and lethal conflict (see Hollimon 1990; Lambert 1993). Lambert (1993) and Lambert and Walker (1991) implicated growing population densities, increased territorial circumscription, and climate change as possible causal factors, but shortages of and anthropogenic impacts on local subsistence resources were likely important factors (Braje 2007). Islanders also increased their reliance on marine fishing and expanded their subsistence economies. Data from each of the three late Middle Period sites with abundant pinniped remains on San Miguel Island (CA-SMI-232, CA-SMI-481, and CA-SMI-528) suggest that islanders focused more heavily on marine mammal hunting. At each of these sites, Guadalupe fur seals dominate the samples, comprising between 36% and 85% of the assemblages by NISP (Table 4). At CA-SMI-481 where age and sex data were reported (Rick 2004, 153), nearly all the Guadalupe fur seal remains were identified as adult females. At CA-SMI-232, we found a similar pattern with a heavy reliance on adult female Guadalupe fur seals.

Kennett (2005), relying on behavioral ecological principles and optimal foraging theory, suggested that the increased hunting of pinnipeds at about 1500 cal BP is related to the introduction of the bow-and-arrow and development of the plank canoe (*tomol*) which made marine mammal hunting a more energy-efficient strategy to feed growing island populations. These technologies probably increased the effectiveness of pinniped exploitation because modern behavioral observations suggest that human hunters on the island would quickly force otariid (fur seals and sea lions) and phocid (harbor seals and elephant seals) populations to Toffshore rocks and outcrops (Allen et al. 1971; DeLong, field observations; Gerrodette and Gilmartin 1990; Riedman 1990; Wilkinson and Bester 1988), where access would be more difficult. Hunting may have only been possible from stable watercraft for in-water or hauled out prey. Landing on offshore rocks such as Castle Rock and Prince Island today is difficult, even with rubberized boats, due to heavy wave energy and the dearth of protected landings. The combination of *tomols* and highly accurate, maneuverable, and powerful bow-and-arrow technology probably allowed hunters better access to easily frightened offshore pinnipeds. The general lack of pup and juvenile remains from island archaeological sites suggests that the large, breeding pinniped populations on San Miguel today (especially at Point Bennett) were not present 1500 years ago. Rather, populations were likely restricted to offshore rocks, and the Channel Islands and western San Miguel only became a breeding and haulout area after the removal of the Chumash during the historic period. Commercial over-hunting and subsequent population recovery seems to have created significant changes in species composition from the prehistoric to modern periods. This seems particularly clear in the near absence of elephant seals, the second most abundant pinniped on San Miguel Island today, in prehistoric assemblages, which are dominated by Guadalupe fur seals that are rare on the island today.

While evidence of a heavy reliance on sea mammals has been documented at the Punta Arena site (CA-SCRI-109) on western Santa Cruz Island (Glassow 2005) and the Eel Point site (CA-SCLI-43) on San Clemente Island (Porcasi et al. 2000) during the Early and Middle Holocene, these sites are located near submarine canyons, which may have allowed for greater access to dolphins and sea mammals. Sea mammal bones also have been recovered in small numbers from many Channel Islands sites predating 1500 cal BP, especially on San Miguel Island where the largest populations are found today (Rick et al. 2005). However, quantification of faunal remains from sites and components older than approximately 1700 cal BP suggests that marine mammals were not the focus of

Table 4. Summary of other San Miguel Island late Middle Period sites with abundant sea mammal bone. Data from Rick 2007 and Walker et al. 2002.

	NISP	NISP%	MNI	MNI%	Adult/ Subad.	Subad./ Juv.	Pup	Male	Female
CA-SMI-481 — 1260–920 cal BP									
Otariidae									
Guadalupe fur seal	47	36.4	12	34.3	37	2	0	2	41
Northern fur seal	23	17.8	8	22.9	21	2	0	0	21
Steller's sea lion	1	0.8	1	2.9	0	0	1	1	0
California sea lion	29	22.5	7	20.0	24	6	0	28	0
Phocidae									
Elephant seal	1	0.8	1	2.9	N/A	N/A	N/A	N/A	N/A
Harbor seal	4	3.1	1	2.9	N/A	N/A	N/A	N/A	N/A
Carnivora									
Sea otter	24	18.6	5	14.3	N/A	N/A	N/A	N/A	N/A
Total	129	100	35	100	82	10	1	31	62
CA-SMI-528 — 1570–1120 cal BP									
Otariidae									
Guadalupe fur seal	85	49.1	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Northern fur seal	28	16.2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Steller's sea lion	4	2.3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
California sea lion	20	11.6	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Phocidae									
Elephant seal	1	0.6	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Harbor seal	3	1.7	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Carnivora									
Sea otter	32	18.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Total	173	100	N/A	N/A	N/A	N/A	N/A	N/A	N/A

the subsistence economy (Kennett 2005,197–198; Walker et al. 2002).

Interestingly, both Rick (2004) and Walker et al. (2002) report decreases in sea mammal remains in Late Period sites on San Miguel Island at CA-SMI-163, CA-SMI-468, and CA-SMI-602. At each of these sites, there seems to be a shift away from a marine mammal to a fish-based economy during the

Late Period (Rick 2007, 136, Figure 7.5; Walker et al. 2002, 631). While only speculative, the decrease in pinniped hunting during the Late Period may be the result of human impacts on and the anthropogenic reduction of marine mammal populations that began about 1500 cal BP. This may suggest that the composition of modern pinniped populations on the Channel Islands are the result of not only commercial over-hunting during the eighteenth and nineteenth centuries but also intensive human utilization that began at least 1500 years ago.

Determining the mechanism that triggered compositional changes from prehistoric to modern pinniped communities on the Channel Islands is of central importance. Cold water episodes during the recovery period after historic over-hunting may have given cold water adapted species such as elephant seals and northern fur seals an advantage over warm water adapted Guadalupe fur seals (Walker et al. 2002, 631). Processes of competitive exclusion or other complex ecological interactions also need to be addressed and will take the cooperative efforts of a variety of scientists including biologists, ecologists, historians, and archaeologists. The first step, however, will be the recognition of the anomalous nature of historic pinniped populations and that their reintroduction to local ecosystems may not have followed "natural" trajectories.

Fascinating new evidence is beginning to emerge, however, that Paleocoastal peoples on San Miguel, Santa Rosa, and Santa Cruz islands may have hunted sea mammals during the earliest occupations of the islands, when human populations were small and sea mammals had little to no fear of human hunters. Recent discoveries at several Early Holocene sites suggest that a finely made, bifacial projectile point technology—Channel Islands Barbed or Punta Arena points—may be evidence of intensive Paleocoastal sea mammal hunting (Braje 2007; Erlandson and Braje 2007; Erlandson et al. 2005; Glassow et al. 2008). Faunal evidence to support this conclusion is currently lacking, perhaps the combined result of rising sea levels, coastal erosion, and the "Schlepp Effect," where sea mammals were butchered on local beaches and not transported to base camps and incorporated into the archaeological record. Ultimately, the question of when sea mammal hunting on the Channel Islands first began and how ancient populations were affected will require continued analysis of faunal and technological evidence from a variety of archaeological sites, isotopic studies from human remains, and DNA investigations from ancient and modern sea mammal bones.

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ALLUVIAL HISTORY AND HUMAN PREHISTORY IN POZO CANYON, SANTA CRUZ ISLAND, CALIFORNIA

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Abstract—A survey in Pozo Canyon on Santa Cruz Island resulted in the discovery of 40 strata of archaeological deposits exposed on the faces of arroyo walls. These exposures result from entrenchment and lateral expansion of the stream channel during the historic period, most likely as a result of increased runoff intensity related to livestock overgrazing. The archaeological strata are distributed among 18 localities along a 2.4 km length of the canyon extending upstream from its mouth at the ocean. All consist of marine shells, mainly California mussel. Variation in stratum characteristics probably reflects degree of disturbance when covered with alluvium and the amount and placement of shells originally deposited by prehistoric people. Strata range in age over a span of 4500 years, the latest occupation being near the beginning of the historic period. The buried archaeological strata reveal that alluvium was accumulating on the bottom of the canyon over at least the last 4800 years and that the canyon bottom was utilized extensively by prehistoric occupants of the island.

INTRODUCTION

Santa Cruz Island is one of four northern Channel Islands located between 20 and 44 km offshore from the south-facing Santa Barbara County coast. It is the largest of the Channel Islands, with an area of 249 km^2, and also the most topographically and environmentally complex. At the beginning of European colonization of California, the island was occupied by Chumash people, who lived in 11 coastal villages. Site deposits on the island are known to date as early as 8700 cal BP (Glassow 2002) and as late as the terminal occupation of the historically documented Chumash people during the first two decades of the nineteenth century (Johnson 1982; Arnold 2001).

The island is an ideal location for investigating the relationship between geomorphic and soil-formation processes on the one hand and prehistoric human occupation on the other. Prehistoric habitation sites are abundant on the island, with the total number estimated to be between 2500 and 3000, and they are relatively evenly distributed throughout the island. A large number of the sites have deposits buried within alluvial or aeolian sediments, indicating geomorphic conditions different from today's. Sediments have a high degree of stratigraphic integrity because they have not been affected by bioturbation via rodent burrowing, which is widespread on the adjacent mainland. Disturbance from tree-throw is restricted to those parts of the island with arboreal vegetation, mainly north-facing slopes and bottoms of ravines and canyons. Other types of bioturbation appear to have had minimal impact, given the typically distinct boundaries between alluvial units, the existence of pedogenesis at the top of many of these units, and intact pebble lines.

Our research focused on the floodplain at the base of Pozo Canyon, located in the southwestern sector of the island (Fig. 1). Prehistoric site deposits are exposed along the arroyo walls of this canyon as horizontal distributions of marine shells, predominantly of California mussel (*Mytilus californianus*). They occur at different elevations above the channel and have varying thickness and density. Rarely are other types of cultural remains present. At the outset, our research had two principal objectives. The first was to determine the relationship between use of the canyon bottom by

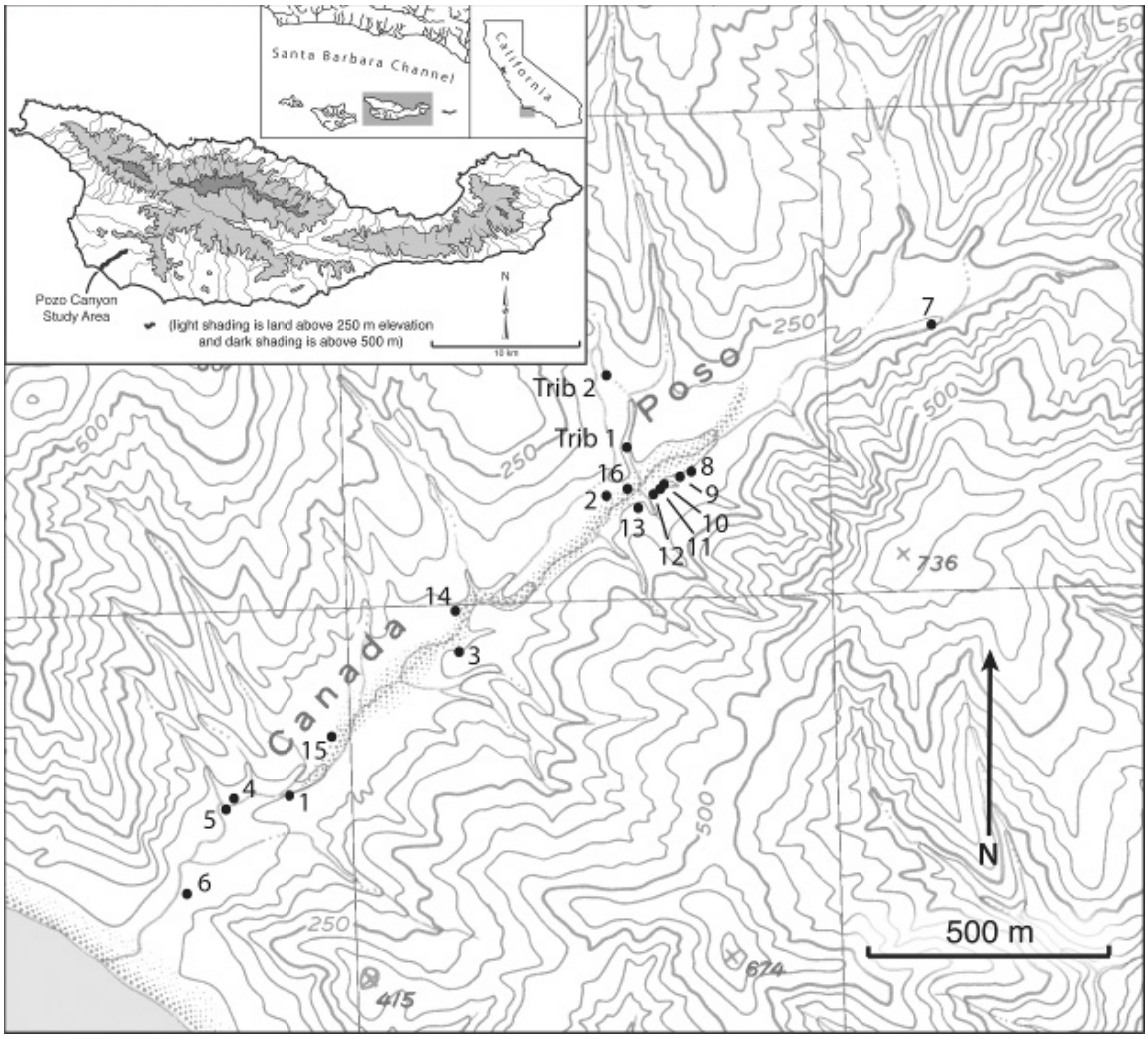

Figure 1. Location of study area and distribution of sites. Only the two sites within the tributary have their prefixes.

prehistoric peoples and the accumulation of alluvial sediments. Was prehistoric use of the canyon floodplain concentrated during particular intervals of time? If so, did these intervals correlate with specific environmental characteristics reflected in the nature and accumulation rate of the sediments? The second objective was to identify any patterning in the geographic distribution of the prehistoric sites that may correlate with geomorphic features, thus providing clues about prehistoric land use. In the course of fieldwork, a third objective was added, as a result of recognizing that historic alluvium occurred at many locations along the length of canyon surveyed. We wished to gain insight into the nature of the historic erosion and alluvial accumulation on the floodplain and the implications for understanding these processes during the prehistoric era.

Pozo Canyon has a gentle gradient and relatively broad floodplain bisected by an entrenched stream channel. Water flows in the channel only during the winter wet season, although perennial surface water is present in the lowermost 150–200 m of its length. Vertical arroyo walls are present along one or both sides of the channel throughout most of its length, and they decrease in height from about 6 m on the upstream end to between 1 and 2 m near the canyon mouth. Today, the floodplain terraces above either side of the active channel are covered with grasslands and coastal-sage scrub. Chaparral occurs on gentle slopes at the terrace-hillslope margins. The incised active channel contains linear groves of willow,

sometimes forming dense thickets. No truly arboreal species are present on the terraces or along the channel. The slopes above the terraces have undergone extensive gullying and sheet erosion, more so than is typical of the island, because of the erodible nature of the soils formed on the clay shale bedrock of the Canada Formation through which much of the canyon is incised (Diblee 2001). The bulk of this erosion occurred during the period of sheep and cattle ranching on the island, which began in the mid-nineteenth century and ended in 1987 (Junak et al. 1995, 35).

Alluvial sediments exposed along arroyo walls vary in texture from coarse sand to clay loam. Localized lenses of pebbles also occur, and a few rock fragments in some of these reach the size of cobbles. Alluvial units typically are flat-lying or nearly so. Infilled channels are rare and are less than 3 m deep. Although distinct intervals of sedimentation and soil development can be discerned along the arroyo, stratigraphic variation in color and texture is not always pronounced. Throughout much of the study area the uppermost stratum of sediments is relatively lighter in color and sometimes laminated, and the division between it and underlying sediments is sharp. These sediments were deposited during the historic period and are a product of intense sheep grazing during the late nineteenth and early twentieth centuries (Brumbaugh 1983). Such capping sediments exist at many locations on the island (Brumbaugh 1983, 108–114). Another indication of historic sedimentation is the presence of abundant large cobbles and stones in the active stream channels. These are largely absent in the alluvium exposed on the arroyo walls. The relatively larger size of these rock fragments is indicative of the higher velocity and volume of streamflow during the historic period.

The prevalence of California mussel shells in the archaeological deposits exposed along the canyon's arroyo walls is not surprising, given that mussel shells typically are the most abundant cultural constituent of prehistoric habitation deposits throughout the island, both along the coast and in the farthest reaches of the interior. Although occupation is known to extend back to 8700 cal BP, most habitation sites for which chronological information exists date after 6000 cal BP. The great majority of recorded habitation sites are located on ridge tops, along the coastal margin, or on marine terraces near watercourses. Consequently, the presence of buried archaeological deposits within the alluvium of Pozo Canyon is of special interest to understanding prehistoric settlement systems.

METHODS

The study of the alluvial deposits in Pozo Canyon and the archaeological strata they contain was part of a larger project concerned with assessing the potential for collaborative research involving archaeology and soil science. The project started with a reconnaissance of several localities on western Santa Cruz Island, and two were selected for investigation, one being lower Pozo Canyon and the other in Cañada Christi (Ballantyne 2006). We selected Pozo Canyon because the initial reconnaissance in 2003 revealed that several buried archaeological deposits were exposed on arroyo walls. During this reconnaissance, three sites were documented, and mussel shells were collected from each for radiocarbon dating. In 2004 we carried out a systematic survey of all arroyo wall exposures in the lower portion of Pozo Canyon to record characteristics of each occurrence of archaeological deposits and to collect additional samples for radiocarbon dates. The survey extended 2.4 km upstream to a point approximately 300 m beyond the last arroyo wall exposure, and it included a tributary with extensive arroyo walls. We recorded 18 sites, two of which were in the tributary. Each was given a numerical designation and a prefix based on whether it was along the main channel (Pozo) or the tributary (Trib). A visit to Pozo Canyon by the senior author and three graduate students in the summer of 2006 resulted in the discovery of one additional site, Pozo 16, and an additional, deeper archaeological stratum at Trib 1.

Documentation of each archaeological site entailed recording UTM coordinates obtained with a GPS receiver; height of arroyo wall; number of archaeological strata; and position, character, and thickness of each archaeological stratum. We also plotted the location of each site on a USGS topographic map and photographed the arroyo wall where the strata occurred. All field records are housed in the Department of Anthropology, University of California, Santa Barbara.

Many segments of the arroyo walls were coated with a thin scum of deposits resulting from rainfall runoff. This scum partly obscured divisions between packets and may have resulted in missing some archaeological strata. However, even at locations where the scum coating was relatively continuous (e.g., at site Trib 1), archaeological strata could be discerned. In such situations we selectively scraped away the scum with a trowel in order to clarify the extent of archaeological strata and determine packet characteristics.

Four sites—Pozo 1, Pozo 3, Pozo 7, and Trib 1 (Figs. 2–5)—were selected for more intensive documentation and collection of shell samples for radiocarbon dating. These were sites with more than two archaeological strata (Fig. 6), and they were spaced relatively evenly through the study area. Shell samples for radiocarbon dating also were collected from two other sites. The date from one of these, Trib 2, complements those pertaining to nearby Trib 1. The other date, from Pozo 16, held the potential to document the earliest visible alluvial deposits, given its location only 10–20 cm above an active channel of the current floodplain. At each of the four sites with multiple archaeological strata, we drew a profile of the arroyo wall that showed major stratigraphic divisions, referred to as "packets." A packet is a distinct alluvial unit. Weak soil development, in the form of organic matter staining

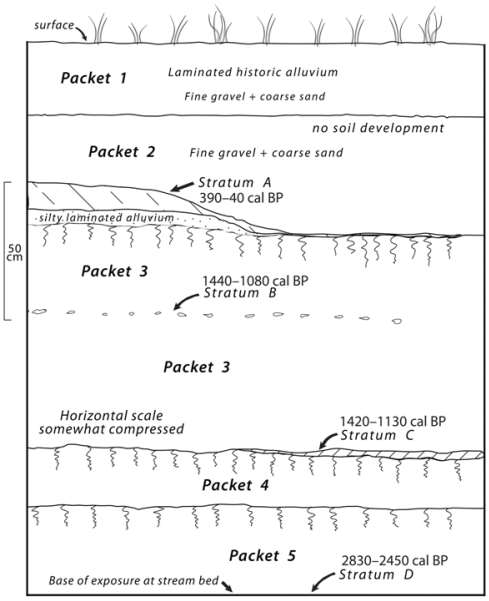

Figure 2. Profile drawing of Pozo 1.

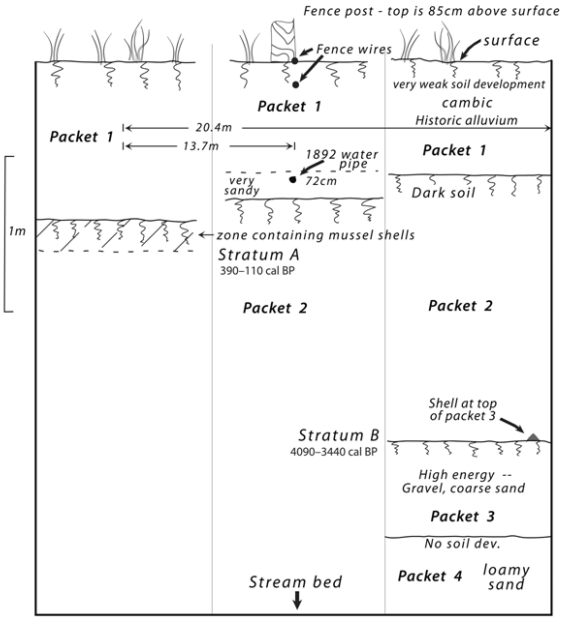

Figure 3. Profile drawing of Pozo 3.

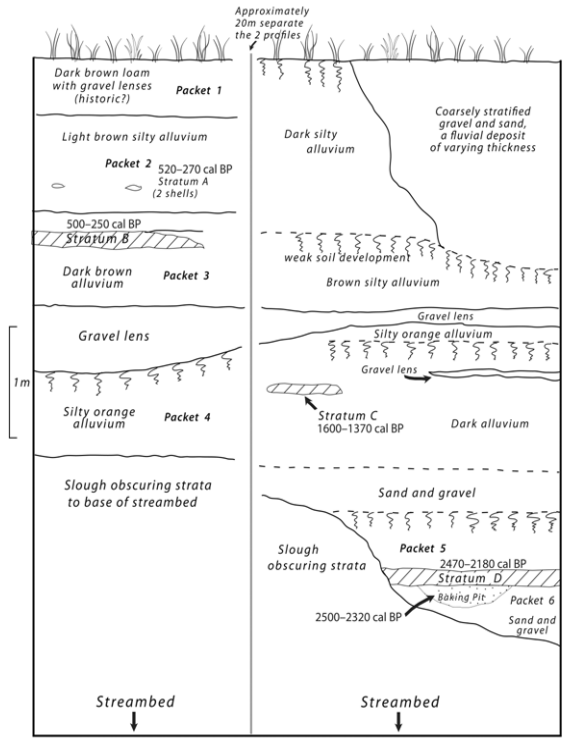

Figure 4. Profile drawing of Pozo 7.

and slight structure formation, often is discernible at the top of a packet. However, packets are distinguished principally on the basis of variation in

color and texture even though minor variation of this sort may also occur within a packet. Also plotted on the profile drawings was the location of each archaeological stratum and positions from which samples were collected. We also photographed each site from which a radiocarbon sample was collected.

Sixteen radiocarbon dates were obtained (Table 1). All but one of the dates were derived from marine shell, either California mussel or black abalone (*Haliotis cracherodii*). If no single shell was large enough for a radiometric date, several fragments from the stratum comprised the sample. Funding was not sufficient for AMS dating. As the dates were derived from marine shell, they were corrected for the marine reservoir effect (Delta R=225±35).

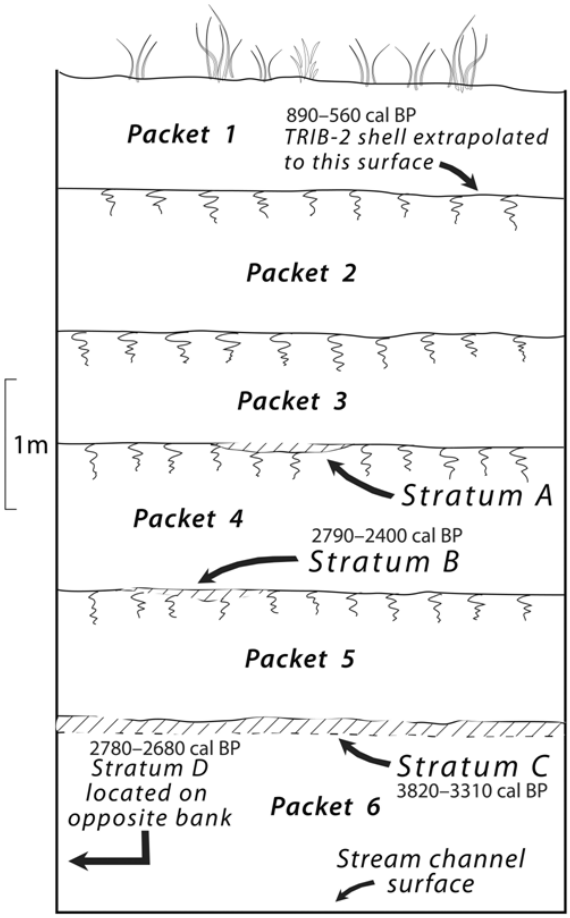

Figure 5. Profile drawing of Trib 1.

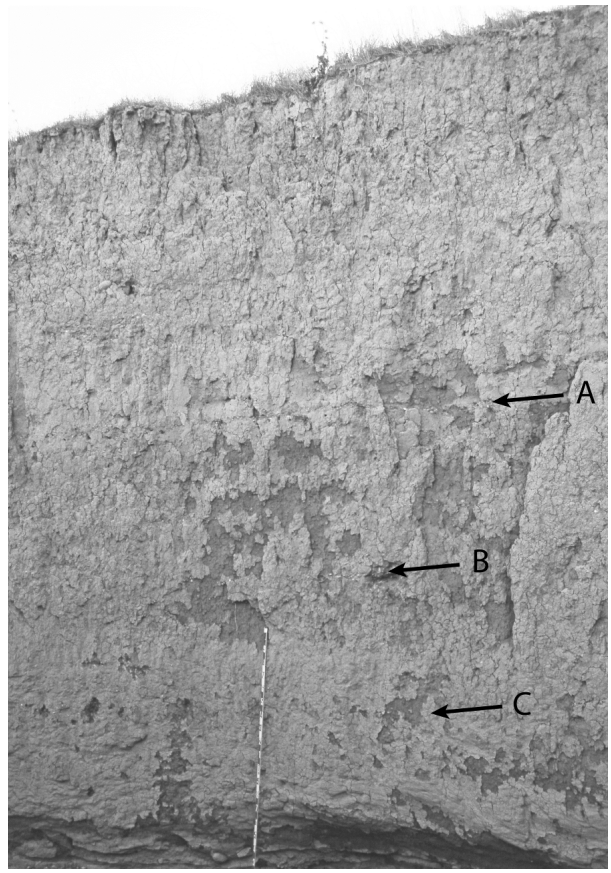

Figure 6. Trib 1 as an example of a site with multiple strata (A, B, C). Pole is 2 m long.

RESULTS

The 18 sites identified (Fig. 1) have a collective total of 40 archaeological strata (Table 2). Seven types of archaeological strata were defined on the basis of thickness of the stratum and dispersion of shell. The breadth of the strata generally is less than 10 m, but in most cases the horizontal extent of a stratum was difficult to follow because of truncation of the arroyo wall, slough against the base of the wall, coatings of dried mud on the wall, or thick vegetation. In the descriptions below, the number of strata within each type is given after each type name.

Low-density middens (16): Thicknesses vary from 5 to 20 cm. Shells in these strata vary in density, but none has a shell density comparable to that of the dense middens of coastal residential bases. These strata most likely are composed of shells at or close to where they were deposited prehistorically.

Thin bands of dispersed shells (9): These strata are 10–15 cm thick, and the density of shells is much

Table 1. Radiocarbon dates.

Lab no.	Locality & depth below surface	Material[1]	C-14 age BP	Conv.age BP	Cal. age BC/AD& 1s interval	Cal. age BP& 1s interval
Beta-185929	Pozo1, Strat A	Several *Mytilus ca*. shells	370±70	790±70	AD 1560(1700)1910	390(250)40
Beta-185930	Pozo 1, Strat B	Several *Mytilus ca*. shells	1500±70	1940±80	AD 510(680)870	1440(1270)1080
Beta-185931	Pozo 1, Strat C	Several *Mytilus ca*. shells	1510±70	1950±70	AD 530(670)820	1420(1280)1130
Beta-185932	Pozo 1, Strat D	Several *Mytilus ca*. shells	2690±60	3130±70	880(760)500 BC	2830(2710)2450
Beta-194823	Pozo 3 Strat A	1 *Haliotis cracherodii* shell	400±50	830±50	AD 1560(1680)1840	390(270)110
Beta-194824	Pozo 3, Strat B	1 *Mytilus ca*. shell	3620±120	4030±120	2140(1790)1480 BC	4090(3740)3440
Beta-194825	Pozo 7, Strat A	1 *Haliotis cracherodii* shell	560±70	990±70	AD 1430(1520)1680	520(430)270
Beta-194826	Pozo 7, Strat B	5 *Mytilus ca*. shells	540±70	950±70	AD 1450(1560)1700	500(390)250
Beta-194827	Pozo 7, Strat C	5 *Mytilus ca*. shells	1750±40	2160±40	AD 350(450)580	1600(1500)1370
Beta-194829	Pozo 7, Strat D, midden above baking pit	Approx. 15 pcs. *Mytilus ca*. shell	2460±50	2870±50	520(380)230 BC	2470(2330)2180
Beta-194828	Pozo 7, Strat D, baking pit	Approx. 20 pcs. wood charcoal	2310±60	2360±60	550(400)360 BC	2500(2350)2320
Beta 234561	Pozo 16	Approx. 100 *Mytilus ca*. shells	4320±60	4730±60	2860(2820)2650 BC	4810(4770)4600
Beta-185933	Trib 1, Strat B	Several *Mytilus ca*. and *Septifer bifurcatus* shells	2680±70	3110±70	840(750)450 BC	2790(2700)2400
Beta-185934	Trib 1, Strat C	Several *Mytilus ca*. and *Septifer bifurcatus* shells	3440±100	3860±100	1870(1600)1360 BC	3820(3540)3310
Beta 234562	Trib 1, Strat D	8 *Mytilus ca*. and 1 *Haliotis cracerodii* shells	2740±70	3170±70	830(780)730 BC	2780(2730)2680
Beta-194822	Trib 2, 70 cm below surface	1 *Haliotis cracherodii* shell	950±70	1380±70	AD 1060(1260)1390	890(690)560

[1]Mytilus ca. = Mytilus californianus.

Table 2. Location of sites and depth, thickness, and vertical position of archaeological strata.

Site	UTM (Zone 11)[1]	Wall height (m)	Hist. alluv. thickness (cm)	Archaeo. stratum depth:max. thickness (cm) A	B	C	D
Pozo 1	0235914E, 3763615N	2.0	25	49:8	93:L[2]	140:L	190:10
Pozo 2	0236538E, 3764218N	5.5	none	280:L	330:L	430:L	—
Pozo 3	0236210E, 3763899N	3.5	70-100	100:20	240:I[3]	—	—
Pozo 4	0235847E, 3763613N	1.8	50	60:L	130:15	—	—
Pozo 5	0235826E, 3763593N	2.2	65-80	120:10D[4]	—	—	—
Pozo 6	0235636E, 3763399N	2.2	50	120:L	—	—	—
Pozo 7	0237193E, 3764577N	6.0	50	110:10	150:10	290:15	450:20
Pozo 8	0236770E, 3764291N	5.2	40	150:15D	440:10D	460:L	—
Pozo 9	0236690E, 3764255N	5.5	40	300:100V[5]	—	—	—
Pozo 10	0236683E, 3764235N	7.4	unclear	470:5	—	—	—
Pozo 11	0236663E, 3764215N	5.2	140	235:10D	275:10D	—	—
Pozo 12	0236634E, 3764211N	2.6	none	120:15D	150:10	175:L	195:10D
Pozo 13	0236552E, 3764157N	5.1	none	2.8:15D	460:15	—	—
Pozo 14	0236222E, 3763983N	2.4	15	150:L	175:L	—	—
Pozo 15	0235915E, 3763650N	1.7	20	50:5	—	—	—
Pozo 16	0236593E, 3764242N	5.5[6]	None	600[6]:5			
Trib 1	0236576E, 3764297N	6.5	none	285:5	400:5	500:15D	600[7]:3
Trib 2	0236570E, 3764476N	5.3	none	70:I	—	—	—

[1]With respect to the 1927 North American Datum.

[2]L = line of dispersed shells.

[3]I = individual shell.

[4]D = dispersed shells within a depth interval.

[5]V = lenses of varying density.

[6]Sample location in streambed about 30 m from an arroyo wall near the location of Pozo 2. Both wall height and stratum depth estimated.

[7]From the opposite bank of the streambed; depth estimated.

lower than in low-density middens. These may represent the margins of strata of the first type, or they may be shells displaced by continual sheetwash from a nearby midden.

Thick band of dispersed shells (1): One stratum is a variant of the previous type. It consists of isolated shells within a band about 100 cm thick.

Band of varying thickness (1): This is another variant. The one stratum in this category contains shell lenses of varying thickness within a band about 100 cm thick. It differs from the one above in containing relatively distinct lenses of shell as well as some isolated shells.

Horizontal lines of dispersed shells (11): In comparison to the types above, the strata assigned to this type have no apparent thickness. They are probably displaced shells from a nearby midden. Each appears to be the result of one alluvial event, or very few events over a short period of time.

Individual shells (2): These are shells isolated from others at the same depth. They may have been discarded by prehistoric occupants, but they could just as easily have been transported by birds that scavenged a shellfish from the coast (see Erlandson and Moss 2001).

Baking pit: A baking pit (pit oven) is bisected roughly in half by the arroyo wall. It is 0.8 m wide and 25 cm deep, and it contains abundant chunks of wood charcoal and fire-affected rocks within a matrix of dark gray deposits. Occurring at the base of Pozo 7, this is the only cultural feature encountered during the survey (Fig. 7). A midden stratum lies directly above the pit, and radiocarbon dates from this stratum and the pit indicate that they are probably coeval (Table 1). The pit and the stratum are counted as one archaeological stratum.

Figure 7. Baking pit near the base of the Pozo 7 profile. Scale's minimum divisions are centimeters.

Alluvial deposition in Pozo Canyon is a product of fluvial processes along the main channel and its tributaries as well as sheetwash and debris flow down adjacent hillsides. The prevailing brownish color (2.5 Y 4/2, 10 YR 4/3) of the prehistoric alluvium exposed on the arroyo walls indicates that aggradation was slow enough to allow soil development to affect in varying degrees all alluvial deposits or alternatively that the source of accumulating alluvium was mainly developed soils eroded from localities within the watershed. The lack of alluvial packets extending throughout the length of the study area is testament to the complexity of alluvial processes.

The relatively distinct boundaries between alluvial packets represent ground surfaces that existed for a period of time before another increment of alluviation occurred. The time interval may have been very short, perhaps only a year, or long enough for some degree of soil development to occur, probably decades or centuries. The number of packets at a site ranged between four and six, and the thickness of packets correlates roughly with the height of arroyo walls. Although packets cannot be correlated between sites, it seems possible that approximately six major episodes of alluvial deposition occurred within the 4500-year interval represented by the suite of radiocarbon dates.

The historic alluvium at the top of the profiles throughout major portions of the canyon represents the last period of deposition. Its light color (10 YR 7/4) compared to the immediately underlying floodplain deposits (10 YR 4/3) is a result of being derived from extensive recent gullying on adjacent hillsides. This gullying cut deeply through hillslope soils with thin A-horizons into the lighter-colored underlying horizons. A significantly greater proportion of the historic alluvium was derived directly from hills and deposited on the floodplain as coalescent alluvial/colluvial fans than was the case in prehistoric times, when the majority of the alluvium was derived from the watershed as a whole and deposited via fluvial processes. The removal of vegetation through overgrazing and the subsequent lowering of infiltration capacity and the increase in overland flow are thought to be driving this shift in

the dominant depositional process within the watershed. The presence of this capping sediment, not only in Pozo Canyon but at many other locations on the island, implies that many canyon-bottom sites dating to the late prehistoric and protohistoric period—sites that would have been exposed at the beginning of the historic period—cannot be observed unless they have been exposed by later erosion.

Although California mussel is by far the dominant taxon represented among the shellfish remains comprising the archaeological strata, shells of other taxa are present. These include black abalone, platform mussel (*Septifer bifurcatus*), limpets (probably most being *Achmaea* spp.), and sea urchin (*Stronglyocentrotus* spp.). Because identification of shellfish taxa is based on rapid visual observation of the exposures on the arroyo walls, it is likely that other taxa also are present in relatively minor amounts. The same may be said about other cultural constituents that often occur in island site deposits. Fish and sea mammal bones and stone flakes derived from knapping may be sparingly present in some of the strata, but they were not recognized during the survey.

The archaeological strata appear to be the result of archaeological items, specifically shells, moving short transport distances as alluvium covered them. The large size of many fragments (some being nearly complete mussel valves), their unweathered appearance, the areal discreteness of the strata, and the concentration of shell fragments comprising each strata all imply short transport distances. In addition, the fine-grained character of the overlying sediments indicates low-energy deposition that favors minimal disturbance to archaeological deposits. Indeed, geoarchaeologists have recognized that archaeological deposits may remain largely intact while being covered with fine-grained sediments deposited under low-energy conditions (Waters 1992, 128, 138–140; Rapp and Hill 2006, 69, 75, 76).

With regard to the different types of archaeological strata, the low-density middens appear to be at or very close to where they were deposited by prehistoric inhabitants. The horizontal lines and various types of bands of dispersed shells appear to be a product of continual alluvial deposition that included removal of shells from a nearby prehistoric site. It is also worth noting that capping with alluvium actually may have increased the preservation of archaeological constituents, as has been noted at certain buried sites on the mainland (Erlandson 2007).

Each archaeological stratum associated with a radiocarbon date gives the maximum age of the ground surface when it was at a particular elevation relative to the current elevation of the stream channel (or to modern sea level). It is possible that an archaeological stratum resided on a former ground surface for several centuries before it was covered with alluvium. Weak soil development at the top of some alluvial packets implies that land surfaces remained stable for such lengths of time. However, many packets lack evidence of soil development, implying that time intervals were relatively short.

Multiple radiocarbon dates were obtained for sites Pozo 1, Pozo 3, Pozo 7, and Trib 1. These are in expected order by depth, although a pair of dates for Pozo 1 is essentially identical as is also the case with a pair for Pozo 7. Apparently each of these pairs is the result of two episodes of deposition from the same archaeological deposit located nearby. Only the date for archaeological stratum D at Trib 1 appears anomalous with regard to vertical relationship with other dates for archaeological strata at a site. This date pertains to deposits exposed along a low bank on the opposite side of the stream channel from the arroyo wall where strata A through C are located. The date for stratum D is close to that for stratum B, located approximately 2.5 m higher in vertical elevation. Because stratum D is separated from strata A through C by a horizontal distance of approximately 3 m, it is reasonable to suspect that a slope existed between the locations of strata B and D, the latter being the result of sloughing from the surface represented by the former. Because the modern stream channel has removed the intervening deposits, this possibility cannot be assessed.

The nature of the archaeological sites represented by the archaeological strata is difficult to ascertain. The limited breadth of the strata implies that sites are small in area, although the transport of site deposits may have been limited to only a portion of the site. The low-density middens, such as those occurring at Pozo 1 and 7, appear to be at or close to the location where site inhabitants deposited food refuse, specifically shells, and their thickness and breadth therefore are most likely to be indicative of

actual site characteristics. Their thickness being 20 cm or less, and their breadth apparently being less than 10 m, indicates that they were camp sites or day-use localities as opposed to main residential bases, and the characteristics of the bands of low-density shells also are consistent with this interpretation. Some of the camp sites may have been occupied for only a period of days or parts of a day, although some of those represented by deposits 10 to 20 cm thick suggest repeated occupation over a period of years or decades based on chronologies of stratified sites elsewhere on the island. If any of the archaeological strata were derived from principal residential bases, their breadth and thickness should be greater, and a greater diversity of faunal remains, including fish and sea mammal bones, should be present.

Many other buried archaeological deposits may exist in the alluvium filling the bottom of Pozo Canyon. Considering that the arroyo walls are, in a sense, narrow transects through the alluvial deposits, the 40 strata are likely a small fraction, the total number possibly being in the hundreds. Furthermore, archaeological deposits may be buried below the level of the current stream channel, the gradient of which is largely governed by current sea level. In a tributary of Cañada Christi, located 3 km north of Pozo Canyon, a midden stratum exposed at the level of its wash dates to 5720 cal BP (Ballantyne 2006, 42), but even earlier archaeological deposits may exist at greater depths in both drainages.

All but 3 of the 18 sites fall within 2 clusters, one located a short distance from the mouth of the canyon and the other near the largest tributary (with 2 branches) within the study area (Fig. 1). The downcanyon cluster is adjacent to the location of a former wetland, indicated by distinctive remnant soil properties including clear redoximorphic features. This wetland undoubtedly would have harbored a variety of plant resources useful to the prehistoric inhabitants of the island. The upcanyon cluster is much tighter, and it consists of the largest concentration of both sites (9) and archaeological strata (21) (Fig. 1; Table 2). This cluster may be a product of one or more factors. First, the arroyo walls are higher and more extensive in the vicinity of the cluster, providing more opportunity for archaeological strata to be seen. Second, the floodplain is broader at this location than anywhere else within the canyon, and consequently vegetation communities are more extensive. These communities may have provided various plant resources, resulting in a greater intensity of human activity. Third, the confluence of the main channel of Pozo Canyon and a major tributary may have been a reliable location of fresh water during the dry season. Today, no surface water exists at this location during summer months, but it may have been present prior to stream entrenchment and degradation of the watershed's water-holding capacity. In weighing these possibilities, the latter two are most plausible: either plant resources or fresh water attracted people to this locality. The greater area of arroyo wall exposures at this location is not as strong a possibility because relatively extensive exposures extend downcanyon of the cluster, yet archaeological strata are absent.

The 16 radiocarbon dates span approximately 4500 years of prehistory. Although this number of dates is too small to discern fluctuation in intensity of Pozo Canyon occupation, five clusters are apparent, the earliest of which is represented by just one date (Table 3). These clusters span an interval of time from the latter part of the Early period to the end of Late period with respect to King's (1990, 28) chronology. None of the clusters matches the few confidently defined date clusters recognized among all radiocarbon dates obtained from Santa Cruz Island sites, aside from the slightly larger number of dates falling within the period between 700 and 250 cal BP. During this time interval prehistoric

Table 3. Radiocarbon date clusters and their correlation with King's chronology.

Interval of group (cal BP)	No. of dates	King (1990) period	King (1990) phases
700-250	5	Late	L1a–L2b
1500-1200	3	Middle	M3–M4
2800-2300	5[1]	Early–Middle	Ez–M1
3800-3500	2	Early	Eyb
4800	1	Early	Eyb

[1]Two of these dates, from Trib 1, probably are of the same stratum.

population on the Channel Islands apparently was highest (Glassow 1999; Erlandson et al. 2001,18–19; Arnold 2001, 41; Kennett 2005, 115–116, 130–133, 159–168). Considering the breadth of each time interval, ranging between 300 and 500 years, the distribution of dates among the later three intervals appears relatively even. This implies that settlement on the canyon bottom was roughly at the same level of intensity during these intervals.

DISCUSSION AND CONCLUSION

The arroyo walls of Pozo Canyon display an impressive series of buried archaeological deposits unmatched in other drainages of the island with entrenched watercourses. The large number of archaeological deposits probably is due to the canyon's relatively flat gradient, a relatively high rate of alluvial accumulation over the last several thousand years, and a moderate streamflow during prehistoric winter storms. The dated archaeological strata span the latter portion of the middle Holocene and all of the late Holocene, during which island populations became increasingly dependent on marine resources and developed sophisticated technology for acquiring them (Kennett 2005).

The 40 archaeological strata demonstrate that groups of people used the floodplain of Pozo Canyon from at least 4800 cal BP to the end of Chumash occupation of the island in the early nineteenth century. Because the island lacks terrestrial mammals that would have been attractive sources of food (e.g., deer or rabbits), prehistoric peoples seeking inland resources would have been interested in either plants or fresh water. If perennial fresh water were available only near the mouth of the canyon, as it is today, then plant foods and materials most likely were the only attraction. The association between archaeological strata and the former wetland and the wider breadth of the canyon bottom supports this hypothesis, as these would have been the locations where seed-bearing and perhaps also bulb- or corm-bearing plants were likely to have been prevalent. A variety of seeds and bulbs or corms are known to have been important food resources among the island Chumash at the time of European contact (Timbrook 1993, 2007). The unentrenched channel also may have supported riparian vegetation, which may have yielded raw materials for house construction, basketweaving, and other industries.

Island inhabitants who created the archaeological strata within the Pozo Canyon alluvium most likely were residents of one of two large habitation sites located on either side of the canyon mouth. Each is over a hectare in area, and each has dense midden deposits 2 m or more in depth. One of these sites (CA-SCRI-474), on the northwestern side of the mouth, was investigated in 1928. This investigation included excavation of a cemetery (Olson 1930; Hoover 1971, 130–168). Circa 1990, Arnold (2001, 42–44) carried out a test excavation at this site. Radiocarbon dates from Arnold's investigation span a period between AD 418 and 1260 (Arnold 2001, 41); that is, most of the dates fall within the 1500–1200 cal BP time interval of Table 3. The other site (CA-SCRI-475), on the southeastern side of the mouth, has not been investigated, and the chronology of its occupation is unknown. Nonetheless, it is clear that neither site was a Chumash village inhabited at the beginning of the historic period. The archaeological strata dating after 500 cal BP were created by people living elsewhere on the island—for instance, at Morse Point 1.8 km southeast of the of Pozo Canyon mouth, where the historically documented community of *Shawa* was located (McLendon and Johnson 1999). Possibly both canyon-mouth sites have deposits associated with the three earlier time intervals indicated on Table 3, but more investigation would be necessary to ascertain this.

Of the approximately 800 documented archaeological sites on Santa Cruz Island, less than 10% are located within canyons, as opposed to ridges overlooking canyons and marine terraces along the coast. Fewer than 20 sites are truly on canyon bottoms, the precise number being difficult to ascertain on the basis of information recorded on site record forms. Only two other canyons, Cañada Christi and Cañada de los Sauces, are known to have extensive and relatively high arroyo wall exposures. Systematic archaeological survey to locate archaeological deposits along arroyo walls has taken place in these two canyons, but only 14 exposures have been located, and only one of these contains more than one archaeological stratum. The abundance in Pozo Canyon appears to be the result of a congruence of topographic circumstances. Only in this canyon is the floodplain bounded by

hillslopes forming the canyon sides, without terraces or other relatively flat landforms elevated above the floodplain upon which prehistoric occupation could take place.

The 40 buried deposits in Pozo Canyon are testimony to the importance of canyon-bottom environments to the island's prehistoric inhabitants. In addition to Pozo Canyon and the other two canyons mentioned, other larger canyons on the island may have, or may have had, archaeological strata buried in their bottomland alluvium. The two most likely possibilities are Laguna Canyon and Cañada del Puerto, but neither has been subjected to archaeological survey. However, these two canyons are associated with the two largest watersheds on the island, and lateral cutting during historic times has removed much of the alluvium on the canyon bottoms, thus reducing the prospect of buried archaeological strata.

The lower prospects in some of the larger canyons on the island should not discourage concerted efforts to locate buried archaeological sites within canyon-bottom alluvium such as those in Pozo Canyon. Many may exist, and they will aid in filling an obvious gap in knowledge of island settlement systems. The sediments exposed on arroyo walls, both in Pozo Canyon and elsewhere, can yield significantly more information about environmental change than we were able to generate in the course of the Pozo Canyon research. Collaboration between archaeologists and soils scientists should continue.

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SOURCE CHARACTERIZATION OF SANTA CRUZ ISLAND CHLORITE SCHIST AND ITS ROLE IN STONE BEAD AND ORNAMENT EXCHANGE NETWORKS

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Abstract—Prehistoric stone bead and ornament industries of southern California are poorly understood relative to the Santa Barbara Channel shell bead industry. Patterns visible in the spatial and temporal distribution of chlorite schist stone disc beads and ornaments suggest well-entrenched, potentially competitive networks of interaction during the Middle to Late Holocene. Retracing the life histories of chlorite-schist artifacts from archaeological deposition to lithic source origin may unveil intricacies of prehistoric politics, economics, and social dynamics not presently apparent in the archaeological record. This paper examines the Santa Cruz Island Chlorite Schist source and its role in stone bead and ornament industries during the Middle to Late Holocene, and reports on the preliminary results of southern California chlorite schist and soapstone/steatite LA-ICP-TOFMS chemical composition analysis.

INTRODUCTION

Over the past several decades, archaeologists working in the greater southern California region have focused on prehistoric exchange networks while recognizing the important role raw materials and crafted items played in the maintenance and creation of social relations (King 1974, 1976, 1990; Blackburn 1974; Arnold 1983, 1987, 2000; Hudson and Blackburn 1986, 1987; Bennyhoff and Hughes 1987; Scalise 1994; Raab and Howard 2000; Howard 2002). Prehistoric exchange networks "strengthened cooperative relationships, group cohesion, marriage alliance, and economic stability" (Rick et al. 2005, 194) while contributing to the developing system of social interdependence that characterized the Late Period in the Santa Barbara Channel.

This study examines one aspect of prehistoric exchange networks in the southern California region. More specifically, this paper will investigate Santa Cruz Island Chlorite Schist in context of stone bead and ornaments exchanged during the Middle to Late Holocene (ca. 5600–1000 BC). Further, it will explore how exchange networks affected local strategies of resource exploitation on Santa Cruz Island. The current study is part of an ongoing research program into stone bead and ornament exchange networks. Using methods of chemical composition, source discrimination, artifact provenience, and GIS spatial and temporal distribution analyses, the research will identify raw sheet-silicate lithic material source locations exploited for stone bead and ornament production, with particular attention to previously identified prehistoric quarries (cf. Heizer and Treganza 1944; Polk 1972; Wlodarski 1979; Landberg 1980; Romani 1982; Parkman 1983, 1985; Williams and Rosenthal 1993; Fig. 1). The overarching goal of the research project is to examine the role of stone beads and ornaments in relation to patterns of prehistoric cultural change between 3000 and 1000 ybp. This paper takes an initial step in that direction by presenting the preliminary results of Laser Ablation Inductively-Coupled Plasma Time of Flight Mass-Spectrometer (LA-ICP-TOFMS) chemical composition analysis on Santa Cruz Island Chlorite Schist, Sierra Pelona schist, and stone bead artifacts recovered from two Middle Period sites in the greater southern California region.

BACKGROUND

The antiquity of stone beads and ornaments in prehistoric California dates as far back as the Early Period (i.e., Eyb, ca. 3500–2400 BC; cf. King 1990, 28). Sheet silicate lithic materials including steatite,

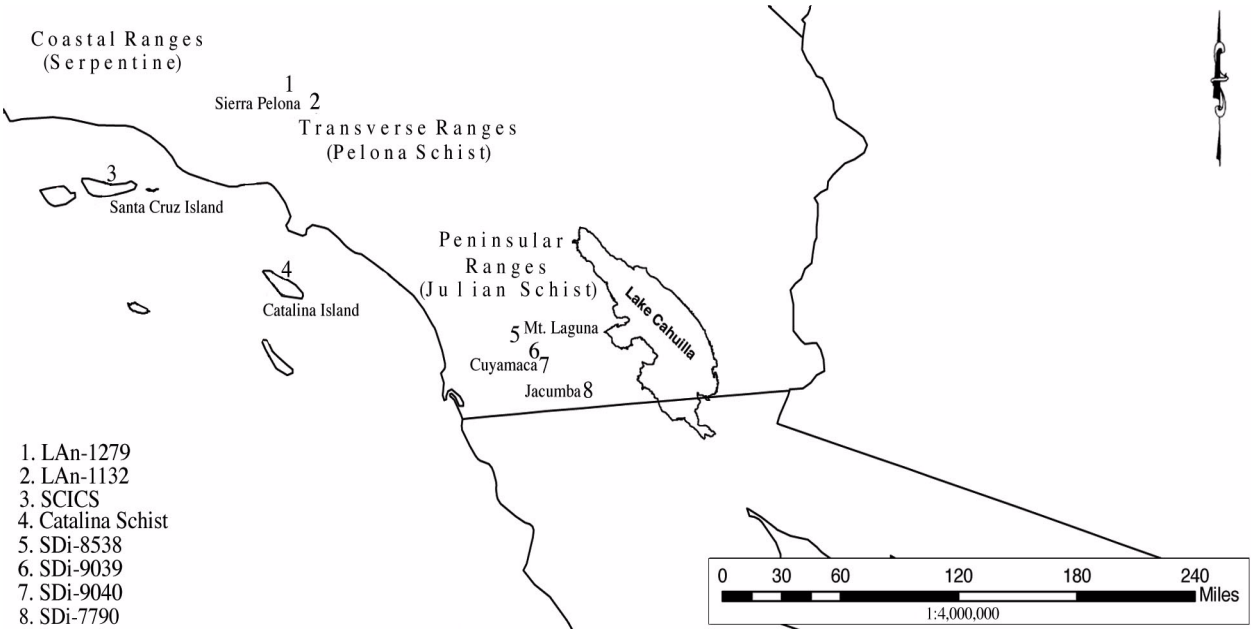

Figure 1. Locations of non-homogenous sheet silicate quarries and raw material deposits in the greater Southern California region.

chlorite schist, talc schist, and serpentine were most often used in stone bead and ornament production, although magnesite, fluorite, argillite, shale, jadeite, siltstone, dolomite, obsidian, and other stone materials have been reported. Among these, chlorite schist disc beads appear to have been most widespread during the Late Holocene. In fact, archaeological data indicates that between 2000 BC to 500 BC chlorite schist disc beads dominated bead assemblages at a number of archaeological sites located in territory historically occupied by Uto-Aztecan (Shoshonean) speakers (King 1983b; 1990, 133; Gibson 1992, 36).

Although shell beads overwhelmingly dominated bead assemblages in the Santa Barbara Channel during the Middle Period, King (1990, 133) noted a change from dark serpentine disc beads to chlorite schist disc beads between M1 and M2a (ca. 800–200 BC). At *Humaliwo* (CA-LAn-264), Gibson (1975, 113–115, Table 3) identified a chlorite schist bead assemblage at levels dated 1000 to 500 BC, which also contained a unique shell bead assemblage. Over 1550 chlorite schist disc beads were recovered from Eel Point C on San Clemente Island, which accounted for 53.97% of the total bead assemblage (Rigby 2000, Table 23.1). A suite of radiocarbon dates from Eel Point C suggests intensive site occupation from 1770 BC to 800 BC (Goldberg et al. 2000, Table 4.2; 1-sigma calibrated; UCLA-2757C thru –2757H), although dates extending from 3250 BC to AD 1000 were also reported (UCLA-2754 and -2757A).

Moving inland, chlorite schist disc beads dominated the bead assemblage at the Chatsworth Walker Cairn Site (CA-LAn-21; see Walker 1951; Romani 1980) in the San Fernando Valley and Vasquez Rocks in Agua Dulce (CA-LAn-361; see King et al. 1974). In San Bernardino County, stone disc beads crafted from meta-sedimentary (chlorite schist) rock were recovered from occupations dating from the time of Christ to approximately AD 1000 at the Ridge Site (CA-SBr-713), which is located in the Cajon Pass (cf. Basgall and True 1985). At Two Bunch Palms (CA-RIV-1246) in Riverside County, chlorite schist disc stone beads dominated the Late Archaic Period (ca. 30 BC–AD 450; Beta-225745 thru -225747) bead assemblage, which included over 120 stone beads (Eddy 2008), and several large Abalone shell beads. Incidentally, no Olivella sp. disc beads were recovered from the deposit (Eddy 2008). In the Western Mojave Desert, Sutton (1988, 44–45) suggested stone beads were fairly common during the Late Prehistoric period from 2000 BC to AD 1650. He went on to argue that the lithic material utilized in bead and artifact manufacture was likely procured from the Sierra

Pelona Schist Formation (Fig. 1), where chlorite and talc schist exposures were reported in the nearby Leona Valley (King et al. 1974a, 1974b; Romani 1982, 31; King 1990, 138, 242; Rosenthal and Williams 1992, 219). Earlier, King (1990, 242) had argued that the Sierra Pelona Schist Formation was a major talc and chlorite schist material source exploited for stone bead and ornament production in the Santa Barbara Channel.

This study will show that locally available lithic material suitable for stone bead and ornament production was not always exploited in productive capacity. Other social, economic, political, or ritual/ceremonial factors may have factored into raw material selection and crafted product exchange. To investigate these issues further, this paper focuses on a relatively unknown source of chlorite schist located on Santa Cruz Island.

The Santa Cruz Island Chlorite Schist Formation [SCISF] is located within the 10-mile long 1-1/4-mile wide belt of metamorphic rock that runs northwest by southeast through the middle of the island (Bremner 1932, 13; cf. Weaver et al. 1969; Hill 1976; Fig 2). This geologic formation accounts for approximately 13% of the island's total surface area and contains within it "dense greenish-gray to brownish gray phyllites or very fine chlorite schists" with localized occurrences of sericite schists and green aphanatic rock or greenstones (Bremner 1932, 13). Dibblee (2001, 1982) describes the lithic material as fine-grained quartz, albite feldspar, and chlorite schist aggregate produced by greenschist-grade metamorphism of volcanic and sedimentary deposits. The schist lacks mica, and contains minor inclusions of epidote, zoisite, actinolite, sericite, hornblende, and titanite. The moderate quartz inclusion makes the schist harder than steatite or pure talc while the high chlorite content keeps the material softer than serpentine. It is therefore highly durable and easily modifiable. In addition, some hand samples have foliations that can be easily separated into thin sheets through hard hammer percussion, which can then be worked into pendant or small beads (Fig. 3). Despite its favorable characteristics, relatively little archaeological evidence of Santa Cruz Island Chlorite Schist exploitation or production has so far been recovered from the island.

Romani (1982) was among the first to research the potential prehistoric use of Santa Cruz Island Chlorite Schist (see also Romani and Romani n.d.). During an exploratory visit to the southern shore of Santa Cruz Island, Romani (1982, 167) identified chlorite schist deposits at Valley Anchorage and Willows Anchorage "similar in appearance to the chlorite schist beads that were used in the Chumash, Gabrielino and adjacent areas." Unfortunately, no attempt was made to chemically discriminate the Santa Cruz Island Chlorite Schist from sheet silicate lithic materials collected elsewhere in the region (i.e., Catalina Island and Sierra Pelona). After completion of the initial field study archaeological research into Santa Cruz Island Chlorite Schist failed to materialize, likely the result of the relatively few chlorite schist artifacts recovered from a handful sites on the Island (M. Glassow, personal communication, May 11, 2007). As a result, important observations regarding the relationship between hunter-gatherer exploitation strategies, material resource availability, and exchange networks were ignored.

METHODS

The methods of data collection are discussed in two phases; 1) field reconnaissance of the Santa Cruz Island interior; and 2) laboratory and statistical analysis. During the field reconnaissance, physical observations were recorded and samples of chlorite schist were collected from the island's interior. The laboratory analysis included microscopic inspection and LA-ICP-TOFMS analysis of chlorite schist samples recovered from the island and a representative sample of chlorite schist disc beads (Fig. 4) from the Chatsworth Walker Cairn Site (CA-LAn-21), located in the San Fernando Valley. In addition to data generated by the current study, an existing chemical composition database was included in the multivariate statistical analysis in order to measure the strength of SCICS chemical affinity, investigate the degree of inter-source group differentiation, and to determine whether any of the stone bead artifacts originated from the SCISF. The existing database included a small number of geologic samples collected from the Sierra Pelona Schist Formation in the Western Mojave Desert and a sample population of chlorite schist and black serpentine or talc chlorite schist stone beads recovered from the Late Archaic Period Occupation

(ca. 30 BC–AD 430) at Two Bunch Palms (CA-RIV-1246), located in Desert Hot Springs. The following section details the strategies of field reconnaissance and sample collection, and the methods of LA-ICP-TOFMS and multivariate statistical analysis.

Field Reconnaissance

Due to the size and scope of the SCISF it was necessary to delineate an appropriate study area, preferably one associated with archaeological sites. The apparent absence of chlorite schist quarries or production loci, arguably difficult to identify in the archaeological record (M. Glassow, personal communication, May 11, 2007), precluded any collection of chlorite schist artifacts in direct association with prehistoric procurement and/or production activities. Despite this setback, naturally occurring deposits of Santa Cruz Island Chlorite Schist were thought to exist in close proximity to archaeological habitation sites. Spatial proximity, or indirect association between deposits and sites, was an important criterion that factored into the selection of a study area. Based on existing archaeological and geologic data, the Central Valley of Santa Cruz Island, specifically Cañada Islay and Cañada del Medio, was selected for the current study (Fig. 2).

Archaeological reconnaissance of Santa Cruz Island's Central Valley was carried out on January 17–19, 2007, and included a pedestrian survey along portions of Cañada del Medio, Cañada Islay, and South Ridge. During the survey, natural sidewall exposures, streambeds, rock outcrops, and hillside slopes were inspected for deposits of chlorite schist. Chlorite schist cobbles and boulders in float were occasionally broken open with a sledgehammer and the interior of the rock inspected for mineral inclusion and weathering. In addition, several archaeological sites located within the Central Valley were visited, including a known Middle Holocene occupation site (SCRI-194). Midden soils exposed on the surface of the sites and surrounding soil matrices were inspected for evidence of chlorite schist in both geologic and archaeological context.

The study area contained a wide variety of chlorite-rich rock including three physical varieties (i.e., phyllite, schist, and greenstone) identified by Bremner (1932, 13–15). Intra-source mineralogical composition of Santa Cruz Island Chlorite Schist also varied, with some specimens containing higher concentrations of fine-grained quartz and others, including greenstone and phyllite, containing higher concentrations of chlorite. Occurrences of epidote and actinolite were also noted. A representative sample of Santa Cruz Island Chlorite Schist totaling 25 specimens was collected from primary and secondary deposits at various locations on the island. UTM collection points were taken for each

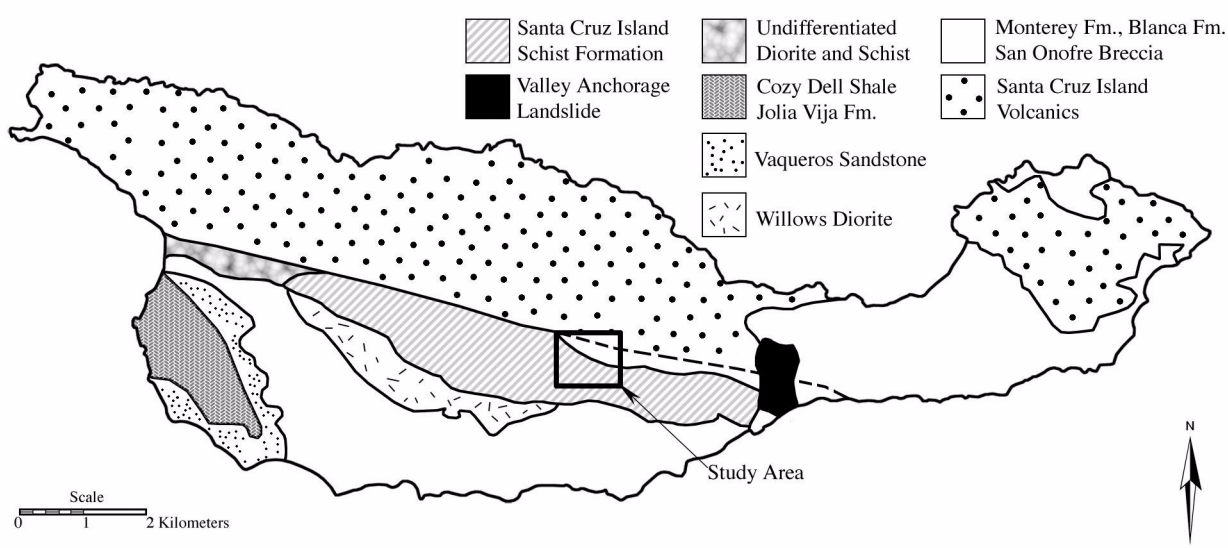

Figure 2. Generalized geologic map showing study area. Geology after Weaver 1969.

Figure 3. Experimentally crafted SCICS pendant shown in various stages of production. A) Percussion flaked schist; B) Ground and shaped on granitic cobble; 3) finished pendant drilled biconically with Santa Cruz Island chert.

primary deposit and several float collection locations using a handheld GPS receiver.

LA-ICP-TOFMS and Multivariate Analysis

The 25 chlorite schist samples collected from the interior of Santa Cruz Island and the chlorite schist stone beads from Chatsworth were analyzed using LA-ICP-TOFMS at the Institute for Integrated Research in Materials, Environments, and Society (IRMES), California State University, Long Beach. To avoid potential discrepancies caused by surface contamination and/or weathering effects and to ensure the samples would fit within the LA-ICP-TOFMS sample chamber a small fragment (no more than 1 cm^2 in size) was removed from the geologic samples. The stone bead artifacts from Chatsworth were small enough to fit within the chamber and, therefore, were not augmented.

Ablations were done over raster patterns approximately 750 $microns^2$ on both the samples and standards. The laser operated at 60% Power using a 100-micron-wide beam at 20Hz, with the laser scan speed set at 70 microns per second. The laser passed over the raster once to ablate any surface contaminations and to "permit time for the sample uptake and for the argon gas plasma to stabilize after the introduction of the ablated material" (Tabares et al. 2005, 22). Samples were scanned once over two runs, or in other words, each element from each sample was measured twice on two discrete areas of the sample. Blanks and standards of known chemical composition (Ohio valley red clay, Brill D, and sm614, 612, and 610) were run at the beginning of each day and after every 10th sample.

Measurements were taken of 45 elements including Na, Mg, Al, Si, K, Ca, Sc, Ti, V, Cr, Mn, Fe, Ni, Co, Cu, Zn, As, Rb, Sr, Y, Zr, Nb, Sn, Sb, Cs, Ba, La, Ce, Pr, Nd, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu, Hf, Ta, Pb, Th, and U. Elements included transition metals and rare earth elements, which were identified as good inter-source discriminators in previous steatite source characterization using Instrumental Neutron Activation Analysis (see Truncer et al. 1998). Quantification of LA-ICP-TOFMS data and methods of source discrimination were also adapted from Truncer et al. (1998). For the current study, inter-source discrimination was achieved by comparing current datasets against the previously generated datasets discussed above.

All elements targeted during the analysis were not detected with equal precision using LA-ICP-TOFMS, therefore the compositional data was screened and those elements with a high number of sample observations below detection limits were removed from the dataset. Element concentrations with high rates of in-group variability were also eliminated. Bivariate plots of elemental concentrations from different source and bead groups were then scanned to identify elements that did not significantly contribute to inter-source discrimination. Based on these screening criteria, 22 of the 45 elements measured (Mg, Al, Si, Ca, Sc, Ti, V, Cr, Mn, Fe, Ni, Co, Cu, Zn, Zr, La, Ce, Nd, Sm, Dy, Er, Pb) were used in subsequent multivariate statistical analysis.

The data from these 22 elements were converted into base 10 log values to "normalize element

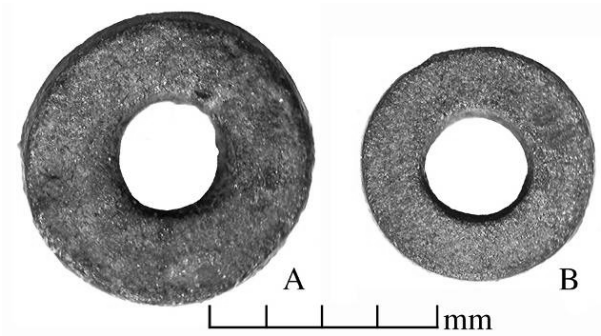

Figure 4. Chlorite schist disc beads from Chatsworth Walker Cairn Site (LAn-21). A) VS-179-1199; B) VS-179-1221.

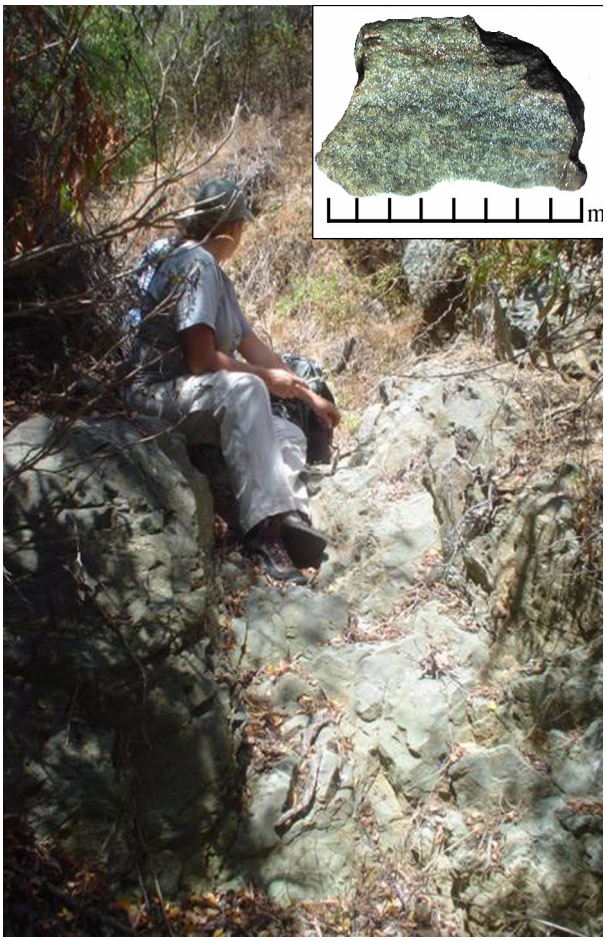

Figure 5. A primary chlorite schist deposit at Cañada Islay. (Inset) Magnified sample of chlorite schist recovered from the deposit.

distributions and reduce the impact of differences in magnitude for some of the major elements" (Truncer et al. 1998, 34). Missing values were substituted using a Mahalanobis distance minimization procedure (cf. Sayre 1975). Logged element concentration values of Santa Cruz Island Chlorite Schist and chlorite schist disc beads from CA-LAN-21 were compared to existing data derived from the LA-ICP-TOFMS analysis of materials collected from the Sierra Pelona Schist Formation and two unknown source stone bead groups identified within the sample population of beads recovered from CA-RIV-1246. Bivariate plots of elemental concentrations from the five groups indicated a high degree of overlap among major elements including Mg, Si, and Al and a moderate to high degree of separation in minor and trace elements including Ni, Sr, Cr, and Sc. Posterior classification based on "Mahalanobis distances from group centroids assuming non-homogenous variance-covariance matrices" was used to evaluate cohesiveness of the compositional groups (Truncer et al. 1998, 34). Canonical discriminant analysis was performed as a further check on the separability of the groups.

RESULTS

During the field survey, several primary chlorite schist deposits in sidewall exposures and secondary alluvial and residual deposits in streambeds and hillsides were identified. Primary deposits of chlorite schist were highly weathered, brittle, coarse to fine grained and of poor to medium toolstone quality. Chlorite schist identified atop South Ridge had practically weathered to clay. Higher-grade chlorite schist deposit was identified in an arroyo on the northern facing slope of Cañada Islay (Fig. 5). This lightly weathered deposit showed signs of erosion due to the heavy flow of water but contained pockets of soft, fine-grained, toolstone grade chlorite schist. Despite concerted efforts, no evidence of prehistoric prospecting or quarrying of Santa Cruz Island Chlorite Schist was noted during the survey.

Although most primary deposits identified in the field were of poor-to-medium quality, fine-grained high-grade chlorite schist, ranging in size from pebble to boulder, littered streambeds throughout Cañada Islay and Cañada de Medio. It is conceivable that the availability of high quality toolstone-grade material in float circumvented any need for laborious quarrying activity, at least in the Central Valley of Santa Cruz Island. In other words, the streambeds, arroyos, and hillside slopes south of the Santa Cruz Island Fault were ideal locations to collect workable cobbles of chlorite schist. Based on these field observations, secondary and tertiary alluvial deposits would have provided an ample source of sheet silicate lithic material for crafting stone beads and ornaments, as well as other types of artifacts including donut stones, effigies, manos, pestles, and other small- to medium-sized non-utilitarian and utilitarian items.

Surprisingly, surface inspections at sites SCRI-194 and SCRI-384 indicated the potential use of chlorite schist cobbles in cooking features with the identification of fire-altered cobbles in the shell

middens. The expedient use of chlorite schist cobbles in fire hearth or cooking features indicates that islanders possessed, at the least, a limited knowledge of the sheet silicate lithic's properties and were aware of the localized resource. Unfortunately, evidence of an intimate knowledge of the stones' properties was not found during the survey. However, several months after the completion of the field study, a chlorite schist pestle was recovered from Site JEP-47, a Mid-Holocene occupation site located in the Central Valley (J. Perry, persoanl communication, December 4, 2007; M. Des Lauriers, personal communication, December 5, 2007). The pestle was apparently broken during manufacture.

Excavations at SCRI-194 also recovered three black/brown stone cylinder bead fragments (Fig. 6) from the upper levels of the shell midden. LA-ICP-TOFMS analysis of the beads identified a strikingly different chemical composition from the Santa Cruz Island Chlorite Schist and other sheet silicate lithic materials (Fig. 7). The stone beads recovered from SCRI-194 were extremely rich in Ca with equally extreme deficiencies of Mg, Al, and Si, major contributing elements of hydrous magnesium silicates (i.e., talc and serpentine) and the chlorite group. Surprisingly, the stone beads recovered from SCRI-194 were not composed of talc, serpentine, or chlorite, the rock-forming minerals most often associated with stone beads and ornaments in southern California. The chemistry of the stone beads suggests they were crafted from calcic amphibolite, common in intermediate to mafic rocks with moderate to high-grade regional metamorphism (Nesse 2000, 279; Deer et al. 1996, 223), or calcic clinopyroxene, which can result from

Figure 6. Stone bead fragments recovered from SCRI-194.

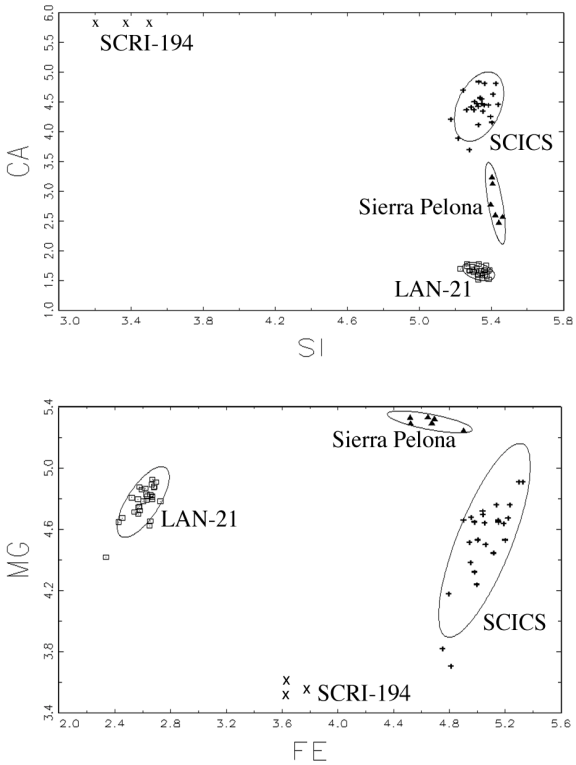

Figure 7. (Top) Separation on bivariate plot (Silicon and Calcium) of SCRI-194 stone beads, LAn-21 and RIV-1246A chlorite schist beads, and Sierra Pelona schist and SCICS source groups. Ellipses indicate 90% confidence level. (Bottom) Separation on bivariate plot (Iron and Magnesium) of SCRI-194 stone beads, LAn-21 and RIV-1246A chlorite schist beads, and Sierra Pelona schist and SCICS source groups. Ellipses indicate 90% confidence level.

the breakdown of amphiboles at high temperature (Nesse 2000, 265). No definite identification can be made at this time, although further chemical analysis may help determine if the lithic material originated from the Catalina Island Schist Formation, the Sierra Pelona Schist Formation, or some other metamorphic geologic formation in the greater southern California region.

Compositional/discriminant analysis conducted during the current study also produced intriguing results for Santa Cruz Island Chlorite Schist. An examination of bivariate plots of canonical discriminant functions (cf. Table 1) calculated for the two source groups—i.e., Santa Cruz Island Chlorite Schist and Sierra Pelona Schist—and the three unknown source stone bead groups indicated good to excellent source group differentiation at the

Table 1. Discriminant-function coefficients by element.

Variable	DCF1	DCF2	DCF3	DCF4
Mg	-.2148	.1706	-.1725	-.4947
Al	-1.0123	.5597	-.3800	.0620
Si	-.8924	2.2180	2.4540	-.8257
Ca	.0156	-.0829	.2961	-.0528
Sc	-.3716	.1541	-.7287	.4421
Ti	-.6882	.6634	-.2251	.1928
V	.2631	-.3604	.2705	-.1019
Cr	.1091	-.0591	-.1223	.0141
Mn	.3225	.1281	-.0468	-.5592
Fe	-.4154	.8482	1.0857	-.2866
Ni	.5208	.4220	-.1495	-.0114
Co	-.3376	.0077	-.1307	.5272
Cu	-.0182	.0060	-.0184	-.0735
Zn	-.0560	-.0742	-.0244	.0746
Zr	-.0184	.0883	-.0874	-.2101
La	.0989	.6029	.7978	-.1919
Ce	-.0510	-.0448	-.3285	-.2463
Nd	.2411	-.2229	-.2514	.1897
Sm	-.0960	-.2076	-.2008	.0172
Dy	-.3076	-.1810	-.1026	.2562
Er	.6466	-.1985	.2885	.0418
Pb	.0078	.1763	.0008	.2887

95% confidence level with all groups plotted. Various combinations of the discriminant functions all showed clear separation between Santa Cruz Island Chlorite Schist and Sierra Pelona schist source groups and two of the three unknown source stone bead groups (Fig. 8). Minor overlap of ellipses of the two macroscopically distinct groups, namely Santa Cruz Island Chlorite Schist and black serpentine or talc chlorite schist stone beads (RIV-1246B), was noted on two of three discriminant function combinations with clear separation noted in the third (Fig. 8). A minor degree of overlap was anticipated during the study given the similar chemistry of hydrous-magnesium silicates, chlorites, and other sheet silicates.

The high degree of overlap and shared elliptical orientation between chlorite schist stone beads recovered from Sites LAn-21 and RIV-1246, on the other hand, suggests the artifacts shared geologic affinity. In other words, the sheet silicate lithic used in bead production likely originated from a common geologic formation, such as the Sierra Pelona Schist or Catalina Island Schist formations. While this does not prove the sheet silicate lithic material originated from a single quarry or source location, it does show that the stone beads recovered from these two mainland sites, separated by more than 130 miles, did not originate from Santa Cruz Island. In addition, the analysis shows excellent separation between the chemical composition of Santa Cruz Island Chlorite Schist and Sierra Pelona schist on all

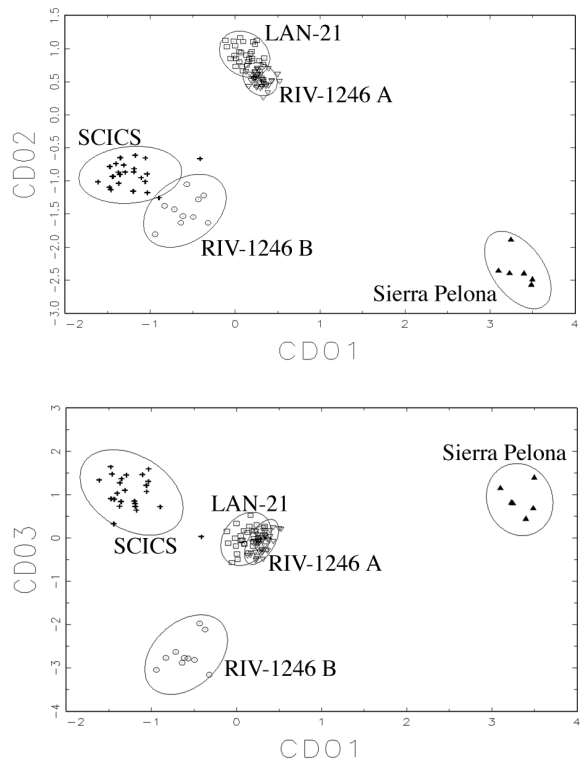

Figure 8. (Top) Separation on bivariate plot (discriminant functions 1 and 2) of SCICS and Sierra Pelona Schist source groups, and LAn-21 and RIV-1246 A & B stone bead groups. Ellipses indicate 95% confidence level. (Bottom) Separation on bivariate plot (discriminant functions 1 and 3) of SCICS and Sierra Pelona Schist source groups, and LAn-21 and RIV-1246 A & B stone bead groups. Ellipses indicate 95% confidence level.

three bivariate plots. Unfortunately the degree of separation, as currently plotted, is likely attributable to the underrepresented sample Sierra Pelona schist, rather than any significant chemical distinction between the two source locations.

To test the degree of inter-group discrimination, a posterior classification of the two source groups (i.e., Santa Cruz Island Chlorite Schist and Sierra Pelona schist) and the three stone bead groups was conducted based on "Mahalanobis distances from group centroids assuming non-homogenous variance-covariance matrices," (Truncer et al. 1998, 34) using cross-validation (Baxter 1994a and 1994b, 201–204) and the 22 screened elements. A classification success rate of 90–100% was achieved for all five groups indicating strong intra-group membership with a high degree of inter-source variability. Despite an apparent geologic affinity, stone beads group membership for LAn-21 and RIV-1246A was consistently distinguished with nearly 100% accuracy. The significance of this distinction has not yet been fully realized.

Overall, the initial chemical composition and discriminant analysis conducted during the current study was successful in its attempt to identify inter-source group distinctions while also identifying intra-source geologic affinity among unknown source groups. The research is a positive step toward chemical sourcing of sheet silicate artifacts to quarries and material source locations in the greater southern California region and promotes future research efforts into stone bead and ornament provenience.

CONCLUSION

To better understand the mechanisms of trade/exchange networks on the island we need to address the issue of why Santa Cruz Island Chlorite Schist was not heavily exploited during prehistory. The quality and abundance of this sheet silicate lithic material indicates that it was suitable for stone bead and ornament production, among other non-utilitarian and utilitarian commodities. This situation is the converse parallel to the island's role in the shell bead and ornament industry during the Late Period, characterized by the mass production of shell disc beads from *Olivella biplicata* readily procured from the island's sandy shore environments. How do we account for the apparent contrast in resource exploitation and production strategies on Santa Cruz Island? Among all possible solutions, the evidence is beginning to point to the existence of strong social and economic ties between the northern and southern Channel Islands during the Middle to Late Holocene, which evolved into region-wide cultural interdependence during the Late Period. Current evidence suggests that Santa Cruz Islanders were reliant upon non-local sheet silicate lithic resources for stone beads, ornaments, donut stones, and other non-utilitarian and utilitarian objects. Aside from the stone beads recovered from SCRI-194, Scalise (1994) noted non-local stone beads and ornaments crafted from talc schist, steatite, and serpentine, near Christy Ranch (SCRI-83) and Prisoners Harbor (SCRI-240). The presence of non-local sheet silicate lithic

materials in stone bead and ornament assemblages on Santa Cruz Island suggests islanders were receiving finished artifacts or raw materials, or both, through established networks, although some argue the Islanders may have traveled long distances to procure the exotic materials directly. Most archaeologists suggest that exchange networks established during the Middle and early Late Holocene emphasized long-distance inter-island maritime trade rather than the more circumscribed mainland-island exchange networks typically associated with the Late Period (Scalise 1994, 600; J. Perry, personal communication, December 4, 2007). The current research supports such claims and may suggest that these prehistoric exchange networks evolved into a "complex set of social, political, and economic factors" (Rick et al. 2005, 195) earlier than once previously thought.

In conclusion, this study demonstrated that intensive LA-ICP-TOFMS chemical composition analysis, coupled with multivariate discriminant analysis, has potential to discriminate the chemical composition of sheet silicate lithic material from multiple source locations. In addition, the method of analysis can identify chemical and apparent geologic affinity between two unknown sheet silicate groups (i.e., stone beads from RIV-1246A and LAN-21). This suggests that sheet silicate artifact provenience is probable, if only on a regional scale (i.e., Santa Cruz Island Chlorite Schist vs. Sierra Pelona Schist vs. Catalina Island Schist).

Conversely, the research failed to link Santa Cruz Island Chlorite Schist to prehistoric stone bead and ornament industries, although the discovery of stone beads at SCRI-194 indicates the Islanders had access to stone bead exchange networks perhaps as early as the Middle Holocene. Despite the results, we cannot simply rule out the possibility of prehistoric exploitation of Santa Cruz Island Chlorite Schist. Further research, including additional LA-ICP-TOFMS analysis of stone beads and chlorite schist artifacts recovered from Santa Cruz Island and the greater southern California region, is desperately needed to test and verify these preliminary results.

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TO AND FRO FOR 67 YEARS: THE STORY OF THE SCHOONER *SANTA CRUZ*

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Abstract—In 1869, Justinian Caire and a syndicate of businessmen from San Francisco purchased Santa Cruz Island. By the 1880s, Justinian Caire took sole ownership and augmented the existing sheep and cattle ranch with a vineyard and other enterprises. By 1893, the need for a dedicated working vessel was apparent, and the schooner *Santa Cruz* was commissioned and built at the Matthew Turner Shipyard in Benicia, California. For the next 67 years, this vessel served the island's owners, ultimately meeting its demise in a nor'easter in December 1960. This paper will review the vessel's history and provide current information on the shipwreck site.

INTRODUCTION

In 1869, a syndicate of San Francisco businessmen purchased Santa Cruz Island, with the intent of developing a ranching venture called the Santa Cruz Island Company. By 1888, Justinian Caire had bought out all shares of this venture, and under his direction the island had a fully operational sheep ranch, as well as extensive vineyards and wine-making facilities. Because of the isolation of Santa Cruz Island, some 26 miles from Santa Barbara, California, there was need for a sturdy vessel capable of withstanding heavy weather and of carrying a wide variety of cargo and passengers. Prior to 1893, the island used the *Star of Freedom*, a two-masted schooner. However, recognizing the need for a sailing vessel with an auxiliary engine, Justinian Caire commissioned the Matthew Turner Shipyard in Benicia, California to build a two-masted gas schooner. This auxiliary power provided aid in both calm and rough weather and when navigating through rivers, harbors, and ports. The schooner *Santa Cruz* steadfastly served its homeport of Prisoner's Harbor for 67 years, earning the honor of being one of the longest operating cargo schooners on the Pacific west coast (Fig. 1).

EARLY OPERATION

The Matthew Turner Shipyard was probably the most well-known and highly regarded of the California shipyards. Currently, there is a California Historical Marker at the site of the shipyard, and portions of the now submerged work platform are still visible at low tide. Originally located in San Francisco, the shipyard moved to Benicia in 1883, where it operated until 1918. In its three decades of operation, the company launched 228 vessels including 169 craft in Benicia, one of which was the *Santa Cruz* (California State Parks 1987).

Recognizing the frequent heavy weather in the Santa Barbara Channel, Justinian Caire told Matthew Turner to "build her strong," knowing that the ship would need to withstand gale force winds

Figure 1. Photograph of the schooner *Santa Cruz*. under sail. Credit: Caire Family Photo Album, Santa Barbara Museum of Natural History.

(Caire 1993, 61; Gherini 2005, 104). The registry certificate on the schooner *Santa Cruz* shows an overall length of 64 ft (19.5 m), beam 18 ft 6 in (5.48 m), draft 6 ft 6 in (1.97 m), and displacement 43 tons (39 metric tons) with one deck and two masts (Gherini 2005, 105). The registry also notes a 40 horsepower gasoline engine. The ship's Log Book Number four reports the Harding Electrical Works in San Francisco built the engine. The registry indicates that possession was taken on May 5, 1893. The first captain was John Revello, a man who had formerly been the captain of the *Star of Freedom,* the schooner used prior to the purchase of the *Santa Cruz*.

In his 1993 remembrance *On Santa Cruz Island*, former ranch hand and one time superintendent (1919–1921) Clifford McElrath alleges that the *Santa Cruz* once served as an Alaskan icebreaker. There is, however, no evidence to support this contention. Rather, Log Book four notes that the first trial was conducted on June 13, 1893 and the final trial just nine days later.

The *Santa Barbara Morning Press* noted in its June 25, 1893 issue that the schooner *Santa Cruz* had recently arrived from San Francisco, which is where Justinian Caire operated his business called the Justinian Caire Company. The story provided her dimensions, identified the captain, and pointed out that the schooner was about to leave for the island. The maiden voyage to Santa Cruz Island occurred on June 27, 1893. Justinian Caire took his wife Albina, his daughters Aglae and Helene, and his granddaughter Maria Rossi (later Maria Rossi Gherini) (Gherini 2005, 105).

By 1893, Santa Cruz Island was functioning as a fully operative ranch, predominantly raising grapes and sheep. Harvested grapes were made into wine on the island, and the *Santa Cruz* was used to ship barrels to Santa Barbara for bottling and sale. In January 1919, however, Prohibition ended the winery business. The Caires continued to export island grapes until the mid-1930s. Other products mentioned in the ship's log included walnuts and almonds and, later, cattle. The *Santa Cruz* could haul 1400 boxes of grapes each weighing 60 lb (27 kg) (Gherini 1983, 9). She could carry up to 250 sheep, but could hold only 15–20 head of cattle until the deck was reconfigured in later years (Gherini 2005, 105). Annually, the *Santa Cruz* carried numerous ranch hands from the mainland to the island to perform sheep roundup and shearing.

EARLY CAPTAINS

The vessel appears to have changed captains frequently during her early years. As noted above, John Revello brought the vessel *Santa Cruz* from San Francisco and captained her inaugural voyage to Santa Cruz Island. Customs records and license documents available from 1897, 1899, 1900, 1903, 1906, 1908, and 1909 show Arthur J. Caire as the sole owner of the *Santa Cruz* and described her as a gas schooner of 43 tons enrolled in San Francisco for the purpose of coastal trading. However, the licenses from 1897, 1899, 1900, and 1903 identify Emmanuele Maggiolo as the master and captain, while the license of 1906 lists James G. Prescott as the captain. George Nidever is identified as the captain on the licenses of 1908 and 1909 (Masters' Oaths 1897–1909).

Margaret Holden Eaton, in her book *Diary of a Sea Captain's Wife*, describes her first visit to her family's camp in Pelican Bay on the north side of Santa Cruz Island in the summer of 1908. She recalled meeting Captain George Nidever, son of the famous sea otter trapper George Nidever, as well as his brother, Jay, and son, Frank (Eaton 1980, 47). The same book references Captain Nidever as captain through at least 1913. One story describes the drowning of George Nidever's brother, Jake, on New Year's Day of that year in Prisoner's Harbor after taking a skiff to the *Santa Cruz* to check her lights, apparently slipping overboard (Eaton 1980, 189). McElrath, who worked at Santa Cruz from March 1919 through 1921, notes that when he took the *Santa Cruz* to the island, she was captained by Giovanni Olivari and crewed by both his son, Pete, and a former Santa Barbara resident, Eduardo, who was a Spanish-Indian man about 60 years old (McElrath 1993, 3). When McElrath left the island in 1921, he noted that the *Santa Cruz* was captained by Mike Negro, whom McElrath called a "young aggressive Neapolitan" (McElrath 1993, 109).

Review of Log Book Number four, spanning from 1914 to 1938, includes the handwriting of several different individuals. Most elaborate and detailed writing extended from log entries dated April 24, 1914 to March 13, 1918. Handwriting

changed from May 23, 1919 until February 25, 1920 and then again February 21, 1923 through October 2, 1929. Unfortunately, the authors did not often sign their names and so the specific identity of the captain's log authors is uncertain.

License documents reveal that George Nidever continued to be the master in December 1911. "Endorsements of Change of Master" documents list Frank Magilio as master in April 1917, Michelo Negro in October 1919, G.B. Olivari in February 1920, Clarence Libby in May 1922, Julius Valdez in January 1923, T. Cornell in July 1923, J. Valdez again in September 1923, and J. Bermudez in January 1925 (National Archives 1898–1935, 1925–1970).

GROUNDING AT RINCON

In her early years, the *Santa Cruz* traveled along the central California coast for periodic maintenance and occasional modifications. She continued to work as a gaff-rigged schooner with a single-screw gas engine and received her servicing at various shipyards in San Pedro, California. Returning home from dry dock in San Pedro, where she had undergone over $1000 in repairs during the summer, the *Santa Cruz* ran aground at Rincon Point, approximately 13 mi (21 km) south of Santa Barbara (Santa Barbara Morning Press 1913).

Santa Barbara's *Morning Press* reported that the *Santa Cruz* ran aground on Friday night, September 19, 1913. Captain Nidever and the crew abandoned the vessel, rowing in the fog towards Santa Barbara. The vessel had been listing heavily and waves were breaking over the deck. Captain Nidever later blamed the grounding on compass error. He noted that he anticipated a one and a half point compass error, but it was actually five points. They rowed the skiff from Rincon Point into Santa Barbara all night, never realizing because of the thickness of the fog that they were actually only a few feet from shore. In fact, they did not even know for certain where they had run aground until the following day when visitors at the Potter Hotel noticed the vessel near the mouth of Rincon Creek (Santa Barbara Morning Press 1913).

On the following day, the *Santa Cruz* was boarded by Mr. and Mrs. A. Raines of Los Angeles, who found the ship's log noting the departure from San Pedro, as well as a pet cat which was still on board. The next day, Captain Nidever returned to the *Santa Cruz* to assess damage. She did not appear badly damaged at that time. On September 23, two launches, *Gussie M* and the *Otter,* attached lines to the *Santa Cruz* in an unsuccessful attempt to pull her free from the rocks at high tide. By the next day, a portion of her keel had floated ashore during high tide, and one of her masts was toppling. The two boats had succeeded only in moving her approximately 19 ft (5.8 m), having difficulty moving her further because of the heavy pig iron ballast. Over the next one to two days, another launch, the *Marguerite* removed the cargo, including the cat, which was later adopted by that vessel. They had filled the *Santa Cruz* with casks in an effort to keep her afloat until a stronger vessel could be obtained from San Pedro. Unfortunately, this boat was also unsuccessful (Santa Barbara News Press, 1988).

Periodic entries in the *Santa Barbara Morning Press* indicate that *Santa Cruz* had not broken up one month later, and an attempt was made to use balloons to free her from the rocks. Unfortunately, this did not work either. Almost three months later, on December 18, 1913, a vessel from the San Pedro Salvage Company owned by Ira T. Fleming was successful in towing the *Santa Cruz* into deep water at high tide. She was then towed back to San Pedro where her engines were reinstalled and repairs were made. In the spring of 1914, the *Santa Cruz* returned to Santa Barbara. The fact that the *Santa Cruz* remained aground near shore for almost three months without thoroughly breaking apart is a testament to the ship building skills of Matthew Turner (Santa Barbara News Press, 1988).

RESUMPTION OF OPERATION

After its repair, over the next 23 years the *Santa Cruz* continued to operate as a cargo and transportation schooner without undergoing significant external changes. On December 23, 1927, the schooner's owners installed new 534-gal (2021 L) gas tanks. Although she was expressly built to handle transportation between the Channel Islands and Santa Barbara, one of the schooner's greatest problems was that her round bottom caused her to roll heavily as the prevailing seas in the Santa

Barbara Channel struck across her beam. Consequently, when a new deepwater port was opened at Port Hueneme, California in May 1942, the *Santa Cruz* became the first vessel to enter there and continued to use this anchorage regularly thereafter. Port Hueneme is located 30 miles southeast from Prisoner's Harbor and offered a calmer passage than Santa Barbara with seas that ran astern (Gherini 1983, 1).

In June 1937, the Caire family sold almost 90% of Santa Cruz Island to E.L. Stanton, a Long Beach oilman. The sale included the schooner *Santa Cruz*. Local newspapers indicated that at over one million dollars, the sale was the largest real estate transaction ever recorded in Santa Barbara County (Gherini 2005, 162). When Stanton took over the island, he evicted Ira Eaton who had been the captain of the *Santa Cruz* in the early 1930s (Eaton 1980, 249), and was operating a camp at Pelican Bay that had hosted numerous movie stars during the preceding 25 years. Red Craine took over as captain of the *Santa Cruz* in 1933, and continued to captain during the first years of the Stanton era, though some sources reference an H. Hoskins as captain between October 2, 1929 and September 28, 1938 (Gherini 2005, 4–5).

Upon taking possession of the *Santa Cruz* in June 1937, Stanton installed a new Buda diesel engine (6LDMR 909 C) with 920-gal (3,482 L) fuel tanks, a 9-ton (8 metric ton) lead ballast keel, and extensive wiring changes including a four outlet fire extinguisher. Over the next nine months a deckhouse was built over the aft cabin, and in September of 1938, an anchor winch was installed. Port of origin was also changed from San Francisco to San Pedro. The Buda engine was probably less than optimal because in April 1942, a new D-13000 Caterpillar diesel engine was installed. This more powerful and reliable engine eliminated the need for sail power, and in April 1943, the main mast and bowsprit were removed. (*Santa Cruz* Log Books four and five).

In July 1947, the Caterpillar engine had almost 4200 hours and was rebuilt. This occurred again in June 1950. Repairs at that time also included a new heat exchanger, new shaft for the fresh water pump and new oil cooler case (*Santa Cruz* Log Book 5). During this period, the deck was also modified as the ranching operation changed from predominantly sheep to cattle. Photographs of the vessel during this period note dramatic changes in the deck with installation of pens to hold cattle. By this time, while the *Santa Cruz* had lost none of her seaworthiness, the graceful sleek lines of her initial design had greatly deteriorated. She maintained this appearance until her loss in December of 1960 (Fig. 2).

FINAL DAYS

Because of her stronger engines, the *Santa Cruz* continued to operate as a motor vessel during the Stanton years. During World War II, she even carried soldiers back and forth to the island. As always, she sailed out of Prisoner's Harbor. When not in use, she would be moored to a buoy 20 to 30 yards (6 to 9 m) from the dock. Prisoner's Harbor generally affords good protection from heavy weather except when "Santa Ana" winds blow from north and east. These winds often originate from a high-pressure zone that forms over Nevada, circulating in a clockwise direction and seeming to come out of the northeast. Weather is usually clear, but seas are exceedingly rough.

On December 6, 1960 at 8:30 a.m. during a "Santa Ana" storm, the *Santa Cruz* drifted from her anchorage onto the rocks at the western edge of Prisoner's Harbor on Santa Cruz Island. The report of marine casualty, completed and signed by Edwin Stanton on December 13, 1960, notes that the vessel was at anchor. Mr. Stanton's son Carey had gone to check the dock at Prisoner's Harbor, which was being battered by heavy seas, when he noted that the

Figure 2. Photograph of the Schooner *Santa Cruz* moored to a buoy at Prisoner's Harbor, Santa Cruz Island, August 1960. Credit: National Maritime Museum, San Francisco.

vessel had parted from her anchorage. In the report Mr. Stanton noted, "It was later discovered that a link in the anchor chain had parted permitting the vessel to drift from her anchorage onto the rocks along the island shoreline. Stanton went on to state, "The vessel was a total loss." At that time, she was valued at $75,000. These statements were reported in the "Oath of Master to Loss Document" filed by Mr. Stanton on December 14, 1960 (National Archives 1935–1970). There is no subsequent mention of the items that were removed from the stranded vessel. However, she was surely lying in shallow water with ample time and ease to remove machinery and any other valuable parts. It is interesting to recall that when she was stranded at Rincon Point in 1913, her value was placed at $3000 with damages totaling $1500 (National Archives 1898–1935).

RECENT SURVEYS OF THE WRECK OF THE *SANTA CRUZ*

In the summer of 1989, both authors were invited to participate in Project Ocean Search sponsored by the Cousteau Society and held for the first time on Santa Cruz Island at Prisoner's Harbor. At that time, The Nature Conservancy was maintaining the western 90% of the island, and the eastern 10% of the island was under the ownership of the Gherini family, descendants of Justinian Caire. Over the subsequent days, with the assistance of others, sketches were made of the wreck site. After completion of Project Ocean Search, several other trips to Prisoner's Harbor were made by the authors to survey, map, photograph, and videotape the site. This effort resulted in a detailed site map with extensive notes. Copies of this data were provided to the National Park Service. This was published as the Submerged Cultural Resources Assessment, authored by Don. P. Morris and James Lima, and published by the Park Service in 1996. This too contained a map of the remaining shipwreck site, though somewhat less detailed than the author's initial map of 1989 (Morris and Lima 1996, 173). For reasons unknown to the authors, the 1989 map was not included in the National Park Service assessment.

Robert Schwemmer of the National Oceanic and Atmospheric Administration (NOAA) completed a photographic survey of the *Santa Cruz* wreck site in October 2007. These photos, when compared with photographs of the vessel prior to sinking, help to document other items previously not identified. Additionally, visits to Santa Cruz Island have identified parts that were removed from the ship including portions of the pile driver onboard at the time of sinking, the two gaff spars, two ventilators, and a ship's lantern. A ventilator and the schooner's compass are on display at the Santa Barbara Maritime Museum.

During the course of research, the authors discovered a hand-written letter in the Santa Barbara Museum of Natural History's library, dated August 12, 1960 and addressed to "Karl" from "Bill," whose last names are unknown (Santa Barbara Museum of Natural History Library 1960). Presumably, however, Karl refers to Karl Kortum, founder of the San Francisco Maritime Museum, an individual who worked tirelessly to discover, save and restore historic nineteenth and early twentieth century vessels. The letter notes a visit by Bill to see the *Santa Cruz* at mooring in Prisoner's Harbor. He noted that the vessel was in good shape but had been considerably altered from its schooner days. He reported that several feet had been cut off the stern and that the mast and spars were on shore. He also reported that below deck the stern cabin appeared unaltered. Bill also talked to Edwin Stanton's son, Carey, who was the primary owner of the island at that time, from whom he received a promise to be notified if Dr. Stanton ever chose to dispose of the vessel. He reported that the vessel usually floated on an even keel but the accompanying photograph taken by Bill was captured just as the boat was rising on a swell (Fig. 2)

Another curiosity discovered by the authors during the Project Ocean Search survey was the finding of the ship's anchor in the haws pipe with chain still attached to the windlass. This would suggest that the *Santa Cruz* actually did not separate a chain link from the anchor causing her to break free, as was reported by Stanton, but more likely separation occurred at the chain or rope to the buoy where she usually moored.

CONCLUSIONS

The gas schooner *Santa Cruz*, built in 1893, played an integral part in the history of Santa Cruz Island during the twentieth century. It served as the main conduit for people, goods, and products to and from the island and had a remarkably long career as a ranching schooner for 67 years. Her ship's logbooks document the ranching history and migration of residents of Santa Cruz Island, while also documenting the military presence in the Santa Barbara Channel during World War II. The schooner withstood extensive modifications, endured a three month stranding on the rocks at Rincon Point in 1913 and weathered numerous storms in the Santa Barbara Channel. While little of the *Santa Cruz* remains in the sands of west Prisoner's Harbor, the vessel's history stands as a tribute to the versatility, adaptability, and perseverance of vessels from the Matthew Turner shipyard.

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MANY SMALL BECOMING MANY LARGE: UNDERSTANDING CHANGES IN CULTURAL LANDSCAPES

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Abstract—On the northern Channel Islands, environmental studies of historical land use tend to be framed with respect to a legacy of environmental impacts and disturbances. Few studies have sought to take the perspective of the historical land user faced with the task of fulfilling land use objectives with the available means while also inheriting the environmental legacies of previous landowners. This paper takes such a tack by tracing changes in fence plans on Santa Cruz Island, California. We use historical maps, documents, field surveys, and a geographic information system to discuss broad changes in fencing plans from a landscape of many small and few large enclosures to one of few small and many large enclosures. We discuss how these spatial changes reflect changes in the functional organization of ranching activities. We argue that changes to cultural landscape artifacts involve the process of *becoming* rather than *appearing* and *disappearing*, which complicates the management of natural and cultural resources.

INTRODUCTION

This paper aims to describe the reasons and means by which ranchers used fences to spatially and temporally partition Santa Cruz Island in the nineteenth and twentieth centuries. While there has been considerable research on the impacts of the island's ranching history on patterns of vegetation and erosion (Junak et al. 1995), there has been little effort to delineate the spatial, temporal, and functional variability of the activity itself. In this paper, we primarily focus on the role of fencing for cattle breeding activities on Santa Cruz. In part, this is because cattle have largely been conflated with sheep as part of a general historical ranching era, even though both developed along different trajectories, reached their peak at different times, and varied spatially across the island. Thus at its most immediate level, this paper seeks to fill this gap by offering a collection of facts regarding the historical and spatial development of cattle ranching on Santa Cruz Island that may help environmental scientists interpret historical impacts to the island.

Beyond the specific relevance of a local history, the paper also aims to discuss a broader problem in studies of cultural landscapes that deals with the shifting semantics of cultural artifacts. On the Channel Islands, cultural resources are often material objects that no longer serve the purpose for which they were made. The reasons for this obsolescence are many: the objectives of the land user may change, there may be new ways of achieving these objectives, or the people who work the land may leave and the ones that follow may not share their values. Whatever the reasons, a landscape will accumulate artifacts that no longer fit the current plan, and at any moment, those charged with the stewardship of the land will be pressed with decisions on what to do with the artifacts of the old days. This is by no means a problem unique to the current management of cultural resources. In this paper, we aim to show how historical changes in ranching plans reflect a general process of cultural landscape change that is defined not by artifacts *appearing* or *disappearing* but rather by one artifact *becoming* something else. This complicates the management of cultural resources as it is perhaps a simpler task to keep artifacts from disappearing than to keep them from becoming something else.

The paper is structured as follows. We begin by reconstructing the origin and change of island fences using four different historical map collections to show changes in spatial configurations between 1850 and 1987. We then present historical evidence to show that broad changes in the twentieth century spatial organization of the island are associated with a novel plan for breeding cattle. We conclude with a

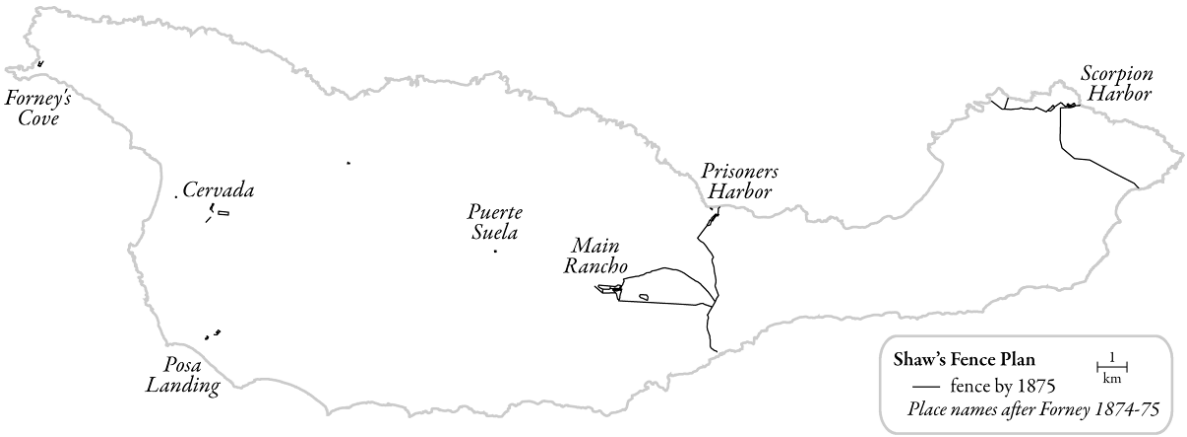

Figure 1. Shaw's fence plan for Santa Cruz Island.

brief discussion of the resource management implications of cultural landscape change.

HISTORICAL FENCING PATTERNS

In this section, we identify four different plans for fencing Santa Cruz Island that were implemented between 1850 and 1987. We used historical maps and field surveys to reconstruct these fencing patterns. Figure 1 shows fence-lines depicted on Stehman Forney's 1874–1875 topographic map of Santa Cruz Island (Forney 1874–1875). We used a digital camera to photograph sections of the original maps at the National Archives, geo-referenced these tiles with a geographic information system (GIS), and then digitized all the fence features. Figure 2 shows all fence-lines depicted on George M. Derickson's series of plats for Santa Cruz Island (Derickson 1918–1919). We made copies from the collections of the Santa Barbara Museum of Natural History and the Channel Islands National Park, scanned these paper sheets, geo-referenced the maps based on ortho-rectified air photos, and then digitized the fence features. We then compared these fence features to those depicted in an older collection of maps made by the Santa Cruz Island Company in the late nineteenth century (Santa Cruz Island Company 1883–1898). In Figure 2, the black lines show fences that also appear in this older collection. We interpret the inclusion of these fences on these nineteenth century maps to mean that these features were part of the ranching plan in the late nineteenth century. In contrast, the dotted lines show fences that are not depicted in this older map collection. We interpret this to mean that these fences were constructed sometime in the early twentieth century.

Figure 2. Caire fence plans for Santa Cruz Island.

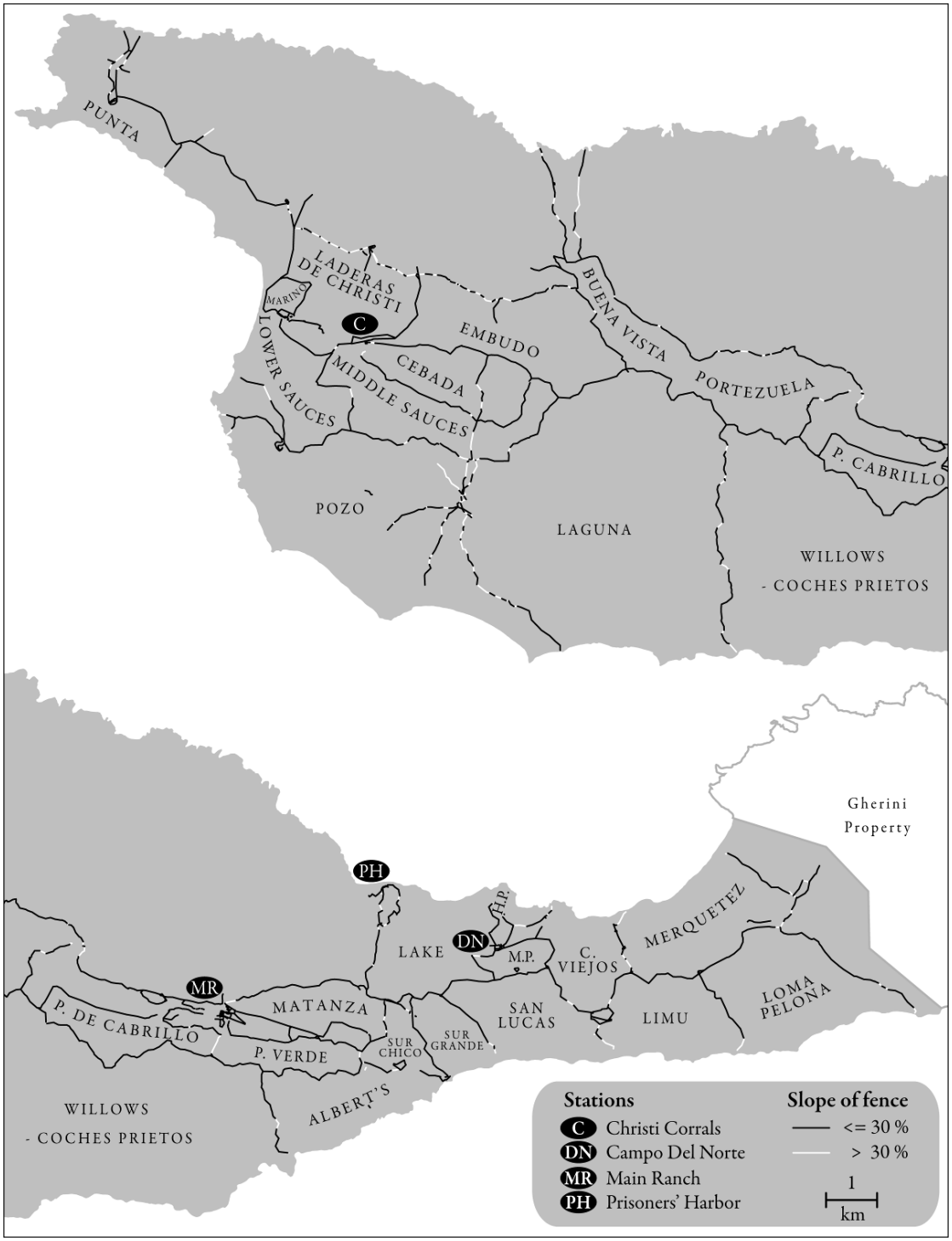

Figure 3. Stanton fence plan for Santa Cruz Island.

Figure 3 shows the fence-lines depicted on a 1964 map of island pastures (Santa Cruz Island Company 1964). We surveyed this fence with a global positioning system, mapped all the vertexes, and then used a GIS to convert these field points into the polylines shown in Figure 3.

Perhaps the simplest way to describe the changes in fence configurations shown in these

three figures is from *many small, few large* to *many large, few small*. The nineteenth century plans seem to consist of few large enclosures and many small enclosures while the late twentieth century plan consists of many large enclosures and few small enclosures. In the next section, we present historical evidence to show that this change in the spatial organization of the island marks not simply the replacement of one land use with another but rather the accommodation of a new plan with the legacy of its predecessor.

MANY SMALL, FEW LARGE

While Southern California was a stronghold for cattle ranching throughout much of the nineteenth century (Dana 1840; Cleland 1941; Menzel 1944), Santa Cruz Island did not mirror this trend. The earliest record of cattle on Santa Cruz Island dates back to April 1830. That is the month that 31 Mexican prisoners were left on the island, "the mission furnishing some tools, cattle, hooks, and a little grain," until a fire purportedly destroyed the encampment and the men abandoned the island on rafts (Bancroft 1886, 48). The fate of the cattle is less certain. In 1851, U.S. Coast Survey Lieutenant Commander James Alden noted: "There are a few cattle here [Santa Cruz], but, like the other islands, there are no inhabitants" (Alden 1853, 105).

Alden was in fact gazing upon private property. Santa Cruz Island was then the possession of Mr. Andres Castillero, who had been granted the island by the governor of Mexico in 1839. Santa Cruz, however, had not been Castillero's first choice. He had originally chosen Santa Catalina but quickly changed his mind, complaining that Catalina was "wholly unfit for cultivation or the raising of stock" (Perez 1996, 32). Still, Castillero did not immediately begin to develop these activities on Santa Cruz. It was not until after 1851, when he employed Dr. James Barron Shaw, that island ranching began. In *Castillero v. US* (340 SD 176), Shaw claimed to have "placed cattle, horses, and sheep on it [Santa Cruz]; built houses and made canals and cut roads on it." His initial stocking program favored sheep over cattle. In 1860, Shaw paid tax on 3 bulls, 72 cows and calves, 116 rodeo cattle, 108 horses, and 12,375 sheep. While the presence of bulls does suggest that Shaw was engaged in a program to breed cattle, this was clearly overshadowed by his sheep program (Gherini 1994; Junak 1995).

After Shaw's tenure ended in 1869, when the island was sold and the Santa Cruz Island Company formed, there was apparently some renewed interest in cattle breeding. The 1869 incorporation letters indicated that the company was formed "for the purpose of engaging in, conducting and carrying on the business of raising Cattle within the State of California and selling and disposing of the same…" (Santa Cruz Island Company 1869). Yet, the assessor records indicate that the company quickly sold off the cattle stock. By 1871, they report only 1 bull, 7 cows, and 96 cattle. The breeding program was apparently halted the following year. In 1872, they report 10 calves and 10 cows, but no bulls. The next year, they report 20 "stock cattle." Over the years, the number of island cattle dwindled as the company focused efforts on sheep breeding. By 1882, the company reported only 7 mixed cows and 1 stock cattle compared with 25,000 common sheep and 37 imported sheep (Santa Barbara County Assessment Tax Rolls 1871–1882).

The design of many small and few large enclosures reflects the plan for achieving the goals of producing wool and mutton given the means available at the time (Fig. 1). The plan divided the island into western and eastern halves with a fence that originated from Prisoners' Harbor. This fence may have been intended to facilitate gathering sheep by keeping them from moving off the isthmus and into the rugged canyons to the west of this fence. In addition, the fence could help direct sheep towards Prisoners' Harbor or Main Ranch during round-ups. The fence on the East End between Scorpion and Smugglers' may have served a similar "funneling" function for Scorpion Harbor. On the western side of the island, the plan consisted of five separate corrals where sheep could be altered or separated for shipment. In general, the fence configuration suggests functions that facilitate gathering sheep but not necessarily excluding them from any places outside a few small cultivated fields.

The specific elements of the fencing plan changed after 1880, when Justinian Caire, one of the original investors in the Santa Cruz Island Company, became sole owner of the Santa Cruz Island Company, but the general strategy of many small and few large enclosures did not (Fig. 2).

Caire sought to improve the function of the sheep corrals scattered on the western side of the island while also introducing the new goal of wine production at the Main Ranch (Gherini 1994; Junak 1995). The plan expanded the extent of cultivation on suitable lands near the western corrals and also enclosed approximately 200 acres for grape cultivation around the Main Ranch. Cattle, however, did not figure prominently into the Caire plan until the beginning of the twentieth century. Ranch records indicate that between 1901 and 1908 the Santa Cruz Island Company constructed the fences shown as dotted lines in Figure 2 (Santa Cruz Island Company n.d.). In total, these new lines enclosed approximately 170 acres of new land for cultivation, primarily around the Main Ranch (~110 acres) and near Christi Ranch (~60 acres). In addition, approximately 2000 acres of new pasture were enclosed with fence. All of these new "potreros" occurred on the west side of the island, particularly in the vicinity of Christi Ranch. While the ledger does not explicitly document reasons for these improvements, it does indicate their coincidence with an investment in cattle. For example, the book includes the entry:

> On the 6th of October 1903 aboard the Pasadena were imported on the Island 302 heifers from Paso Robles… Some of the older unused to sheep ground broke their backbone on the Potrero Norte barrancas…

The phrase "sheep ground" suggests that land previously used for pasturing sheep was now being used for cattle. The book also indicates that bulls were imported to the island during this time, suggesting that the Santa Cruz Island Company had again imparted on a program for cattle breeding.

However, if the new fence was part of a plan for breeding cattle, it does not appear that it sustained the function of enclosing space over time. On November 11, 1916, the superintendent wrote to the island owners:

> We would like instructions relative to the amount of fence work we should do. There is a lot of this work to be done and one place is about as important as another. It will require the expenditure of considerable money in labor and material. Fully one half of the fence around the Potrero Norte will have to be replaced. At Christi practically all of the wire on the old fences is rusted out and the same applies between Scorpion and Smugglers … (Santa Cruz Island Company 1916–1920)

Work repairing fence was a common refrain in this weekly correspondence between island superintendent and absentee owner. By November 1917, the Potrero Sauces fence had blown down, built just 10 years earlier. In November 1918, the superintendent wrote:

> We have fence and road repair work for at least 26 men for a year. If you can send good men they will be very welcome. We have had too many of the other kind lately. The force of men now on the Island is not sufficient to keep up with the routine work (Santa Cruz Island Company 1916–1920).

Thus, the fences that appeared as lines on the late nineteenth and early twentieth century maps did not effectively delineate one space from another on the island itself over time. The men struggled to maintain the many small enclosures of corrals and fields, while few large enclosures actually functioned to exclude or contain animals.

FEW SMALL, MANY LARGE

In 1937, the Santa Cruz Island Company was sold to Edwin L. Stanton. Between 1954 and 1962, the Santa Cruz Island Company constructed nearly 180 km of fence, roughly the distance from Santa Barbara to Long Beach. This statistic is even more impressive when it includes a measure of the slope of the land that the fence traverses (Fig. 3). More than 22.5 kilometers of the fence crosses over land that exceeds 30% slope. Anyone who follows this line, particularly the lines on the western portion of the island, will appreciate the remarkable effort that it took to build this fence. At every place the line changes course, you will find that the men built a solid brace, shaped like a double H, using railroad ties and redwood posts. In all, they built more than 2700 of these braces.

While most of the fence built under the Stanton tenure was new, in the sense that lines appeared in

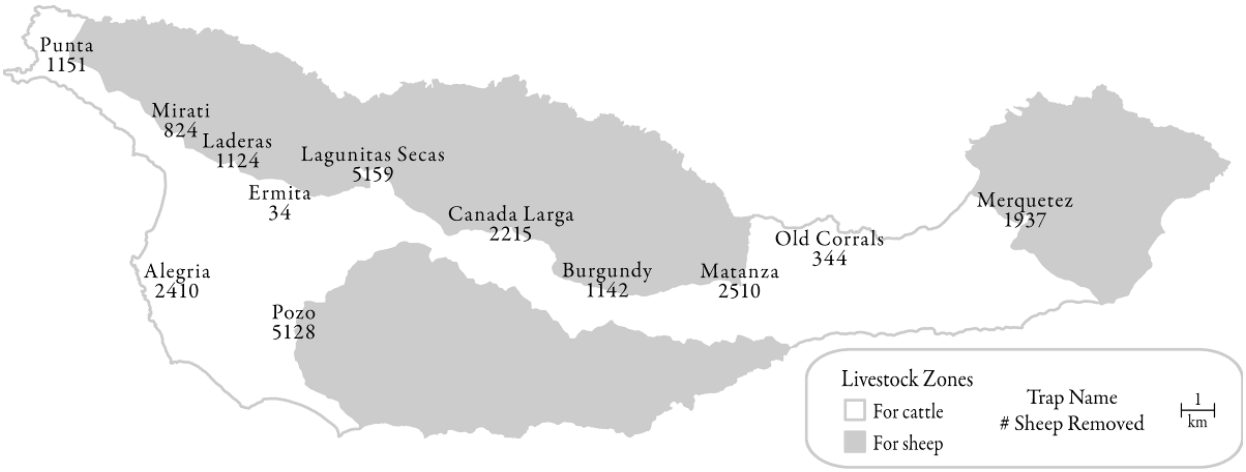

Figure 4. Clearing sheep between 1956 and 1962.

areas where no fence had been built previously, the materials used in the construction of the lines themselves were often taken from the earlier fences. This shows that the Stanton plan adapted the previous plan in a literal sense: by re-purposing the material artifacts that were left over from the old days. In particular, the braces of the H-post vertexes were redwood posts that had been salvaged from the earlier lines. On many of these, you can still find the cut nails and pieces of the old, thick gauged wire that distinguish the nineteenth century lines. In addition, a few old lines were adopted into the new configuration. This includes the east line of Matanza and the line that divides Embudo and Christi pastures. These older lines are characterized by a higher frequency of redwood posts (the earlier lines did not use metal posts) and either a more meandering line (without distinctive vertexes) or the use of X-braces at the vertexes (rather than H-posts).

This re-purposing of material artifacts also corresponded with a change in the semantics of the animals that the fence functioned to either exclude or contain. Stanton's goal was to breed cattle, while sheep no longer served their original purpose as a means for producing wool or mutton. Thus the Stanton plan called for conserving the island's available forage for cattle, which meant that they needed to control the amount of grazing pressure that any area endured. To do this, they had to first clear sheep from the portions of the island that would be most suitable for cattle. After clearing, they needed to keep the sheep from returning and then move cattle from one pasture to another in order to sustain the pasture's function for providing forage.

The Stanton fence was thus designed for these various ends. The plan included twelve different "traps" that were used to clear sheep. Between 1956 and 1962, Santa Cruz Island employees carried out 108 individual "corridas" to remove more than 24,000 sheep from a contiguous strip of land running from Punta to Merquetez (Fig. 4). They focused on clearing the relatively gentle sloping lands on the isthmus, in the Central Valley, and along the west and southwest coasts. They did not clear sheep from the more rugged terrain along the south and north shores. Thus, they created an island for cattle bordered on three sides by sheep, which meant that they needed to maintain these boundary fences in order to keep waves of sheep from spilling back in. Some pastures apparently "leaked" more than others. For example, the fence between Pozo and Laguna crossed some particularly rugged terrain (Fig. 3), making it difficult to maintain, as can be seen in the number of sheep removed from Pozo by The Nature Conservancy between 1978 and 1987 (Schuyler 1993). It should be noted that under Stanton's plan the sheep did not so much lose their purpose as acquire a new one. They became a means for hunting and, beginning in the early 1960s, the Santa Cruz Island Company derived a reliable income from a private hunting concessionaire.

Yet the Stanton plan did not simply divide the island into land for either cattle or sheep. Rather, it partitioned the island at a spatial granularity that mapped to the functional granularity that is embedded in the language that ranchers use to

describe cattle breeding activities. The Santa Cruz Island Cattle Books, kept by Dr Carey Stanton between 1954 and 1987, describe actions carried out on different kinds of cattle: bulls, heifers, cows, calves, weaners, culls, and so on (Santa Cruz Island Company 1954–1987). The recurring activities of cattle breeding involve putting bulls with cows, separating bulls from cows, calving, branding calves and castrating bull calves, weaning and culling calves, and shipping culls. This cycle was controlled by the decision of when to put the bulls with the cows. On Santa Cruz, this decision was made based on the rancher's knowledge of the island's precipitation patterns, island topography, and rangeland vegetation. About 94% of the island's rainfall generally comes between November and April (Boyle and Laughrin 2000). Because of this, Stanton's plan for Santa Cruz consistently put the bulls with the cows in the middle of February, often around Valentine's Day, so that the cows would begin calving as the grass began growing the following fall. As a result, the round-ups for marking and castrating calves were consistently carried out in March, while the round-ups for weaning and culling consistently occurred in August–September.

To efficiently use the transverse shape of the land for cattle breeding, the plan parsed the cows into two sub-units. The following discussion refers to place-names shown in Figure 3. One sub-unit herd was pastured in the mid-east isthmus section of the island and utilized the Campo del Norte corrals for round-ups and brandings. The other herd was based on the island's western end, and round-ups and branding were done at the Christi corrals. Meanwhile, the bulls were kept in the small pasture between Matanza and Potrero Verde in the Central Valley for most of the year. On the west side, cows were frequently put in Sauces and Christi for rearing and calving. On the east side, Lake (Del Norte), Old Corrals, and Merquetez (Mielquieres) pastures frequently served these functions. Summer pastures were Pozo, the Point, San Lucas, and Loma Pelona. Cows were rarely put in the Central Valley, which kept them separated from bulls. In addition, cows were rarely put in the rugged South Side pastures. These rugged pastures, such as the Laguna, Coches, Willows, and Matanza, were used more frequently for fattening younger animals, including both heifers and steers. Calves, however, were not put in these rough terrains. When they needed to be weaned from their mothers, they were often put in Cebada and Mount Pleasant (M.P.) pastures.

Due to the island's rugged terrain and limited road system, most of the cattle moving and gathering was done by vaqueros on horseback. Quasi-permanent groups of horses were based at both Del Norte (in the horse pasture, "H.P.") and Christi (in the Marino pasture). Horses were almost always kept at both places though not necessarily the same individuals. In general, for the vaqueros, a typical day's work with the cattle fell into two broad patterns. During breeding and calving season they rode the pastures checking on the condition and health of animals. For round-ups, they would head out at first light to the farthest reaches of an appropriate pasture and then gather the animals back toward the corrals, often finishing at dusk. The animals would be held overnight and then run through the corrals the next day. After the spring round-up, the animals would be left another night near the corrals in order for the cows and calves to pair back together. Shipping activity was more common in the fall. Bulls from the west would be driven to the Main Ranch and then down to the Prisoners' Harbor corrals, while culls from Del Norte would be driven through the Lake (Norte) Pasture to the Harbor the day before shipping so that that animals could be loaded early in the morning. Interspersed with this work would be riding the fence lines to check for repair needs or seeing that the water supplies were functioning.

In March 1988, following the death of Dr. Stanton, The Nature Conservancy assumed total control of island management and the Stanton land use plan came to an end. In the last round-up, the cows and their newborn calves were gathered from Sauces and Christi pastures on the west and Del Norte (Lake) and Old Corral pastures on the isthmus. They were taken to the Harbor, run through a squeeze chute that had been brought there for the event, and then shipped off the island.

The appearance of fennel as dominant land cover has been one of the more noted changes to the landscape since the last round-up (Beatty and Licari 1992; Brenton and Klinger 1994; Dash and Gleissman 1994; Colvin and Gleissman 2000). Fennel is particularly dense in pastures that were used for calving over the winter of 1987–1988, before the animals were shipped off the island, and

Figure 5. Campo Del Norte corrals, 1974 and 2008.

in the old corrals at Del Norte and Christi. Figure 5 shows the Del Norte corrals at two different moments in time. The top photo shows the corral in 1973 while the bottom shows the same location in 2008. In the foreground of the older photo, you can see fennel stalks that appear trampled. There are also a few isolated patches of fennel stalks on the hills behind the corrals, but the vegetation cover there is notably low and open. The fence stands tall in comparison. In the more recent photo, the cover in the foreground has been mowed by a machine and the hills behind the corral are covered thickly with fennel. Pictures from the west end show a similar story. Figure 6 shows the Christi corrals in 1982 (top) and 2008 (bottom). It is possible that the recurring pattern of the fall round-up—bringing animals to and from the Del Norte and Christi corrals in August, when fennel was in seed—facilitated the dispersal of fennel into pastures that were used to separate the cows and calves. However, the persistent use of the pastures limited the cover through constant grazing pressure. With the removal of cattle, this dispersal vector may have ended (replaced by vehicles along roads), but so too did the grazing pressure that limited the dominance of fennel.

CONCLUSION

In this paper, we have shown that the fence constructed by the Santa Cruz Island Company after 1954 facilitated a system of land use with no precedent in the previous hundred years of ranching on Santa Cruz Island. For much of this history, Santa Cruz was a landscape of many small and few large enclosures. The mid-century fence was part of an innovative plan to breed cattle on Santa Cruz facilitated by a landscape of few small and many large enclosures.

Both the unintended and intended consequences of this plan are manifest in many vegetation patterns that can be seen on the island today. While fennel patterns may be one of the plan's more notorious unintended consequences, many island visitors may be surprised to learn that the distinctive vegetation

Figure 6. Christi corrals, 1982 and 2008.

boundary along the east line of the Loma Pelona was generated by a land use system instigated by ranchers in the mid-twentieth century. It would seem prudent at the very least to continue delineating the spatial, temporal, and functional pattern of land use history on Santa Cruz to better understand these very different kinds of environmental legacies.

This paper has also brought to light the shifting semantics of a plan's material elements that complicate the management and preservation of cultural resources. The pieces of nineteenth century fence that were used to anchor the vertexes of Stanton's fence provide tangible evidence that land use change does not involve one artifact *appearing* and another *disappearing* so much as one artifact *becoming* something else. In this sense, there was continuity in the cultural process of landscape change when The Nature Conservancy adapted the Stanton fence as part of their Pasture Improvement Program that removed sheep from the property (Schuyler 1993). The fence has now deteriorated to the point where it no longer serves a practical value. It will, perhaps, only be preserved into the future if it is re-purposed from functional to symbolic value as a practical landscape becomes picturesque.

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CLARENCE BROCKMAN LINTON (1880–1925): CHANNEL ISLANDS ENTREPRENEUR, ORNITHOLOGICAL COLLECTOR, AND PIONEER MARICULTURIST

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Abstract—Clarence Brockman Linton (1880–1925) was a little-known naturalist and Channel Islands entrepreneur at the beginning of the twentieth century. His multiple interests included ornithology, archaeological pot-hunting, and abalone pearl mariculture, activities by which he made his living. From 1907 through 1910 Linton concentrated his efforts on Channel Islands birds, during which time he collected and sold at least 1061 bird skins, and a small number of egg sets from Santa Cruz, San Clemente, San Nicolas, and Santa Barbara islands—more than any other Channel Island bird collector. His specimens, representing 97 species, are currently housed in 21 museums around the world. Linton also published 11 island-related articles in the ornithological journals, *Condor* and *Auk*, before he was 30. His ornithological work adds to the body of knowledge about the birds of the California Channel Islands, and provides specimens and important information relative to the distribution and status of birds on these islands during the early part of the twentieth century. In January 1909, while excavating Indian burials on San Nicolas Island, Linton came across 13 immense pearls he deduced had come from red abalones. According to Linton, "These average the size of an English walnut, and if freshly taken from the shells would be worth easily $3500." Excited by new economic possibilities, Linton redirected his island interests to the business of abalone harvesting and pearl mariculture. He purchased the 60-foot power cruiser, *Flyer*, and by 1911 had secured rights to offshore waters at San Clemente, San Nicolas, and Santa Barbara islands. His mariculture efforts were the first attempted in southern California. Linton's pioneering pearling venture was so successful that for a time he owned a jewelry store in Long Beach from which he sold his cultured abalone pearls. By 1914, however, Linton had abandoned all involvement with the California Channel Islands. He separated from his wife and moved to Seattle in 1918, before returning to California where he died in 1925 at age 44.

INTRODUCTION

The late 1800s and early 1900s was a period of discovery and intensive collecting of specimens from the California Channel Islands. During this period, most of the birds endemic to the Channel Islands were first described. Also, the majority of birds collected from the Channel Islands that are today housed in museum collections around the world were collected during this period. While most collectors were individuals working for colleges, universities, or museums, there were a number of individuals who actively collected specimens for their own private collections, or for sale to public institutions or other private collections. Clarence Brockman Linton is one of the least known of these private collectors.

Clarence Brockman Linton (1880–1925) was a self-trained naturalist, curio collector, ornithologist, and pioneering mariculturist, who developed a great interest in the California Channel Islands in the early 1900s. During a time when the three largest islands were privately owned and title to the remaining five rested with the U.S. government, Linton found unique ways to make his living on the islands, despite being neither an owner nor a primary government lessee. From 1907–1910 he collected bird specimens to sell to public institutions and to individuals who maintained private collections. His four years of fieldwork resulted in

significant contributions to knowledge of Channel Islands ornithology. Today Linton's specimens are found in at least 21 institutions and museums worldwide. In 1909 Linton refocused his island interests to raising pearls in abalones, thus becoming California's first mariculturist. Although he enjoyed a modest amount of success at this pioneering venture, he gave up his island mariculture business within six years. This paper summarizes the southern California life of Clarence Brockman Linton and his important Channel Islands ornithological contributions and pioneering pearl mariculture venture.

BIOGRAPHICAL SKETCH (1880–1925)

Clarence Brockman Linton (Fig. 1) was born in Illinois on October 4, 1880 to Sarah and Horace Linton (1847–1921). Horace had married Sarah Brockman in Jackson County, Illinois on February 6, 1879. The family moved to Kansas, and in 1887, when Clarence was 6 years old, his family moved west to Whittier, California, where they were a part of a group of families who established a Quaker colony (Sanford 1978). Linton attended local schools and graduated from Whittier College (*Daily Enterprise*, October 10, 1967). On January 22, 1905, at the age of 23, Linton married Blanche Eliza Lashlee (1883–1976) of Nebraska, although that marriage ended in divorce.

Figure 1. Clarence Brockman "C. B." Linton (1880–1925).

Between 1905 and 1907, Linton developed an interest in the California Channel Islands. At the time, the three largest of the eight islands were privately owned, and the other five were government owned, with leases granted to private individuals. Joseph G. Howland (1862–1923), manager of Santa Catalina Island for William Banning, held leases to San Clemente Island (1901–1918), San Nicolas Island (1909–1919), and Santa Barbara Island (1909–1914; Daily 1987), and it was undoubtedly through a relationship with Howland that Linton gained legal access to these leased islands. In 1907 he made five trips to San Clemente Island and two to Santa Cruz Island with the owner's permission in order to collect birds (Table 1). Letters in the Smithsonian Archives confirm that Linton corresponded with prospective buyers before and after his island trips: October 29, 1907 "Dear Mr. [Alex] Wetmore, …I have just returned from 3 weeks on San Clemente Island collecting for myself and Drs. Bishop and Dwight of the [Cooper Ornithological] Club. I have a pair of San Clemente wren, rock wren, horned lark, song sparrow, and towhee to exchange…"; and November 17, 1907 "Dear Mr. Wetmore, …I am leaving tonight for 4 weeks on Santa Cruz Island and will write you when I return…" (Smithsonian Institution Archives, Record Unit 706, Box 36, Folder 3, C. B. Linton correspondence 1907–1908). Linton was accompanied on this November 1907 trip to Santa Cruz Island by his stepfather, Horace Linton, ornithologist George Willett, and craw fisherman "Cold-foot Jorgensen" (Linton 1908b). Permission to camp and to collect birds on the island was granted by Mr. Fred Caire, owner of the island (Linton 1908b). During this trip the field crew collected birds and camped at Coches Prietos, Potato Harbor, Northwest Harbor and in the pines near Prisoners' Harbor (Linton 1908b). The following year, 1908, Linton returned to Santa Cruz and San Clemente islands at least three more times each, and to San Nicolas Island once (likely without permission), to collect additional specimens.

The year 1909 was particularly significant for Linton and his island enterprises: Joseph G. Howland's San Nicolas Island and Santa Barbara

Table 1. Dates when Clarence Brockman Linton was collecting birds on the Channel Islands.

Date	Island	Published article
January 23–February 19, 1907	San Clemente Island	Linton (1908a)
March 7–April 7, 1907	San Clemente Island	Linton (1908a)
May 12, 1907	San Clemente Island	Linton (1908a)
May 17, 1907	Santa Cruz Island	
July 2, 1907	San Clemente Island	Linton (1908a)
October 5–October 21, 1907	San Clemente Island	Linton (1908a)
November 7–December 23, 1907	Santa Cruz Island	Linton (1908b)
January 9, 1908	San Clemente Island	
March 7, 14, 30–April 1, 1908	San Clemente Island	
September 26, 1908	San Nicolas Island	
September 29–October 27, 1908	Santa Cruz Island	
November 5, 1908	Santa Cruz Island	
November 14–December 12, 1908	San Clemente Island	Linton (1909)
December 19, 1908	Santa Cruz Island	
January 1, 1909	Santa Barbara Island	
January 1–15, 1909	San Nicolas Island	
April 5, 1909	San Nicolas Island	
May 5, 10, 13, 1909	San Nicolas Island	
June 12, 1909	San Clemente Island	
July 4–5, 1909	San Nicolas Island	
October 14–15, 1909	Santa Cruz Island	
March 27–June 5, 1910	San Nicolas Island	

Island leases commenced in 1909, thus affording Linton legal access to these islands. It was during a trip to San Nicolas Island that Linton discovered a cache of large pearls. In October 1909 he sublet a portion of Santa Barbara Island from Howland for $125 for the propagation of pearls in abalones. Thus Linton redirected his focus from collecting and selling ornithological specimens to developing a mariculture business for abalone pearl, meat, and shell, and began to establish camps on a number of the islands for this new business. By the end of the year, Horace and Sarah Linton had divorced, and Horace took a job tending sheep for Howland on San Nicolas Island. With his stepfather working on San Nicolas Island, Clarence had access to the island to pursue his commercial interests in specimen collecting and pearl mariculture.

Early in 1910, Linton met and married Texas-born socialite, Lillian T. McClelland (1888–1977) (Sanford 1978; Fig. 2), and they spent their 3-month-long honeymoon in a rustic tent camp on San Nicolas Island. The former glove-wearing society-bride adapted to the harsh conditions of camping on an isolated island. During their stay on the island, Linton advanced his search for Indian artifacts (Fig. 3) and collected and prepared bird specimens for sale (Fig. 4). A pregnant Lillian maintained the camp (Fig. 5) and assisted Clarence with collecting birds (Fig. 6). Lillian also kept brief notes in a 1910 diary, preserved in the family by their granddaughter, Nancy Hudson, and donated in 2008 to the Santa Cruz Island Foundation. In it, Lillian mentions daily events and describes camp life: "March 30 got water from 2-1/2 blocks away, took abalone meat from shells to look for pearls; May 28 C[larence] found Indian skeletons; May 29 cooked my first cake for supper with sea gull egg. It was fine; June 5, C[larence] skinned a fox" (L. Linton unpublished manuscript). Meals on the island included fried abalones in corn bread, lemon tapioca pudding, hotcakes, beans, dried apricots, potatoes, and bread. One meal prepared on April 5, 1910 by Linton's Mexican cook consisted of laysan albatross (*Phoebastria immutabilis*) stew, much to

Figure 2. Lillian T. McClelland (1888–1977). Photo from Clarese Prior.

the chagrin of Clarence Linton, who salvaged the bird's severed head for his collection (Peters 1938; Fig. 7). This is the first and only known specimen record of this species from any of the California Channel Islands.

After their extended honeymoon, the Lintons took up residence in Long Beach, California. Within four years they had three children: Clarence McClelland "Mack" (1910–1990); Theresa (1911–2005); and Marian (1913–c. 1920). The Lintons separated sometime around 1918, and Clarence moved to Seattle. Although Lillian joined him for a brief reconciliation, after the death of their youngest child, Marian, they both returned to Los Angeles where they lived separately until Linton died in 1925 at age 44 of tuberculosis. (N. Hudson, personal communication). Clarence Brockman Linton is buried in Hollywood Forever Cemetery (Section 12, Plot 15), Los Angeles, California next to his second wife, Lillian. Of their surviving children: Mack graduated from Stanford University and University of Southern California law school; and Theresa attended Otis Art Institute in Los Angeles and became a regionally popular artist.

Figure 3. Clarence Linton excavating Indian burials on San Nicolas Island. In 1909 he discovered a cache of large pearls, which led to his interest in mariculture.

Figure 4. C.B. Linton preparing birds at his camp on San Nicolas Island, 1910.

LINTON AS ORNITHOLOGICAL COLLECTOR, 1907–1910

Beginning in 1907 and continuing through 1910, Linton developed a commercial bird collecting operation on the Channel Islands and along the adjacent southern California mainland. Linton visited four of the Channel Islands (Santa Cruz, San Nicolas, Santa Barbara, and San Clemente islands) on numerous occasions to collect

Figure 5. Lillian Linton at camp during her honeymoon on San Nicolas Island, March–June 1910.

Figure 6. Lillian Linton with shotgun used for collecting birds seen here with her companion, "Doc," during her honeymoon on San Nicolas Island, 1910.

birds (Table 1). He collected his first bird, an island horned lark (*Eremophila alpestris insularis*), at San Clemente Island on January 19, 1907, and his last bird, a snowy plover (*Charadrius alexandrinus*), at San Nicolas Island on May 24, 1910. During this 4-year period, Linton collected a total of 1061 scientific study skins from 97 species (Appendix A). He was the most prolific of the collectors of Channel Island birds: the birds he collected represent 12.1% of the 8,754 birds known to have been collected from the Channel Islands (P.W. Collins, unpublished data). Linton collected a few egg sets from the islands; however, his principal focus was collecting bird skins. Linton sold birds collected from the Channel Islands to a number of individuals who maintained private bird collections and to a number of public institutions. Today his Channel Islands bird specimens are housed in 21 museums: 17 in North America and 4 in foreign countries (Table 2). Five of these museums (Museum of Comparative Zoology, Field Museum of Natural History, Los Angeles County Museum, Museum of Vertebrate Zoology, and British Museum of Natural History) hold 86.6% of Linton's Channel Islands bird specimens, with the Museum of Comparative Zoology at Harvard holding the largest percentage (61.8%, n=655 specimens; Table 2).The majority of birds collected by Linton were collected on San Clemente and Santa Cruz islands, with additional specimens collected on San Nicolas and Santa Barbara islands (Appendix A).

Linton collected a total of 97 species, including 60 species from San Clemente Island, 22 species from San Nicolas Island, 63 species from Santa Cruz Island, and 5 species from Santa Barbara Island. His collections spanned all taxonomic groups, including 19 species of marine/aquatic birds (9.9%); 12 species of shore birds (10.1%); and 66 species of land birds (79.3%; Appendix A). Twelve species of land birds (12.4% of all species collected) and over half of his Channel Islands specimens (55.5% or 589 specimens) were endemics to the islands (Appendix A). The most commonly collected species were song sparrow (*Melospiza melodia*), spotted towhee (*Pipilo maculatus*), horned lark (*Eremophila alpestris*), island scrub-jay (*Aphelocoma insularis*), Bewick's wren (*Thryomanes bewickii*), house finch (*Carpodacus mexicanus*), wandering tattler (*Heteroscelus incanus*), rock wren (*Salpinctes obsoletus*), orange-crowned warbler (*Vermivora celata*), hermit thrush (*Cathrus guttatus*), and sage sparrow (*Amphispiza belli*; Appendix A). Eight of these eleven species or subspecies were island endemics. Linton also collected a number of specimens that represent either first records or only known records for several species on the Channel Islands. These include laysan albatross from San Nicolas Island; yellow-billed cuckoo (*Coccyzus americanus*) and canyon wren (*Catherpes mexicanus*) from Santa Cruz Island; and long-eared owl (*Asio otus*), red-naped sapsucker (*Sphyrapicus nuchalis*), summer tanager (*Pringa rubra*), rusty blackbird (*Euphagus carolinus*), and Harris' sparrow (*Zonotrichia querula*) from San Clemente Island.

Three land bird endemics found on San Clemente Island may have been impacted as a result of Linton's collecting. Between 1907 and 1908, Linton collected 35 Bewick's wrens (*Thryomanes bewickii leucophrys*), 94 song sparrows (*Melospiza melodia clementae*), and 71 spotted towhees (*Pipilo maculatus clementae*) from San Clemente Island.

Figure 7. Laysan albatross head (MCZ 316509) salvaged by Linton from a specimen which had been killed and cooked for supper by the Mexican 'camp cook' at San Nicolas Island on April 5, 1910. Photo by Brian Burd.

Table 2. Museums holding bird specimens collected by Clarence Brockman Linton from the Channel Islands off the coast of southern California.

Museum	Number of specimens
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts	655
Field Museum of Natural History, Chicago, Illinois	123
Los Angeles County Museum, Los Angeles, California	52
Museum of Vertebrate Zoology, University of California, Berkeley, California	45
British Museum of Natural History, Tring, England	43
Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia	24
American Museum of Natural History, New York, New York	18
California Academy of Sciences, San Francisco, California	16
San Diego Natural History Museum, San Diego, California	14
University of Kansas, Museum Natural History, Lawrence, Kansas	14
Museum für Naturkunde, Humboldt University of Berlin, Berlin, Germany	14
Denver Museum of Natural History, Denver, Colorado	10
Cornell University Museum of Vertebrates, Ithaca, New York	10
Carnegie Museum of Natural History, Pittsburgh, Pennsylvania	5
Royal Ontario Museum, Toronto, Canada	4
University of Michigan, Museum of Zoology, Lansing, Michigan	4
University of Washington Burke Museum, Seattle, Washington	3
Smithsonian, United States National Museum, Washington DC	2
University of Nebraska State Museum, Lincoln, Nebraska	2
University of California, Los Angeles, California	1
Peabody Museum of Natural History, Yale University, New Haven, Connecticut	1

This intensity of collecting undoubtedly contributed to the decline of these three island endemics, which are today extirpated from the island. The extent to which over-collecting or habitat loss from overgrazing by feral herbivores led to the extirpation of these three island endemics on San Clemente Island is unknown. However, both factors likely contributed to the extinction of these taxa on San Clemente Island.

Although family recollections record that Linton attended ornithology classes at Whittier College (N. Hudson, personal communication). Linton had no formal training as an ornithologist; however, he was an active member of the Los Angeles branch of the Cooper Ornithological Club. He published a total of 11 papers relative to his work with Channel Island birds. Of particular note are three papers that summarize information about the birds he collected on San Clemente and Santa Cruz islands in 1907 (Linton 1908a and b) and on San Clemente Island in 1908 (Linton 1909b). Most of Linton's other papers are short notes about a particular species' distribution or taxonomic status (Linton 1908c–g, 1909a), or about its nesting habits (Linton 1911a and b). After publishing the first three papers related to birds observed and collected on San Clemente and Santa Cruz islands, Linton did not publish any additional overview papers about the seasonal status, distribution, or abundance of birds on these islands. However, he continued collecting birds on the islands throughout the rest of 1908 and all of 1909 and 1910. Birds collected

during this later period not only contributed additional specimens from previously collected species to museum collections, but also documented new distributional records for several of the islands. A number of these island records have not previously been published, because most of Linton's Channel Island specimens were largely housed in private and foreign collections that were not readily accessible to ornithologists. Thus, they were overlooked by Alfred Brazier Howell when he prepared his seminal publication on the birds of the islands off the coast of southern California (Howell 1917), and by Joseph Grinnell and Alden H. Miller when they prepared "The Distribution of the Birds of California" (Grinnell and Miller 1944).

LINTON AS CALIFORNIA'S PIONEER MARICULTURIST, 1909–1914

In 1909 Clarence Linton began to redirect his business interests from ornithological collecting to that of culturing pearls in abalone shells—a decision spurred by his discovery of thirteen walnut-sized pearls buried with bones of Native Americans on San Nicolas Island (*Los Angeles Times*, February 1, 1909). While excavating remains of Indians on San Nicolas Island, Linton discovered the remains of a chief around whose neck were found "thirteen immense pearls, each one with a small hole drilled in the smaller end for stringing" and which were the "size of an English walnut and if freshly taken from the shells would be worth easily $3500" (*Los Angeles Times*, February 1, 1909). Linton felt that the pearls came from red abalone, an important source of food for Native Americans that lived on the island. When he returned to the mainland Linton placed these pearls on exhibit at the Hotel Virginia in Long Beach (*Los Angeles Times*, July 15, 1909).

By the summer of 1909 Linton had collected enough pearls to warrant his pursuit of an abalone pearl mariculture business on the Channel Islands. The process of culturing pearls from abalones involved "drilling a hole through the shell center, pushing a round ball made from shell, and filling the outside end of the hole with beeswax and cement." (Edwards 1914). Linton established a number of island camps (Figs. 8–9) on San Clemente, Santa Barbara, and San Nicolas islands through arrangements made with J.G. Howland, and he employed Japanese divers (Figs. 10–11) to plant the seeds for pearl growth in black abalone beds. His island employees also harvested abalone meat and shells (Fig. 12). By 1910, Linton had amassed enough pearls to open a jewelry store in Long Beach (Fig. 13). In September 1911 Linton purchased the 60-foot power-cruiser, *Flyer* (Fig. 14), to service his island interests (*Los Angeles Times*, September 28, 1911). He was familiar with *Flyer*, as he had chartered the vessel at least twice in 1909 to take members of the Cooper Ornithological Club, of which he was a member, on birding expeditions to the Channel Islands (*Los Angeles Times*, June 26, 1909 and July 8, 1909).

Figure 8. Linton established camps on several islands to support his commercial operations.

Encouraged by his success, Linton filed Articles of Incorporation on behalf of his C.B. Linton Investment Company on February 15, 1911. The company reported capital stock of $30,000 and named incorporators and subscribers: C.B. Linton, J.W. Wood, Peter McClelland, F. Earl Brown, and J.C. Brown (*Los Angeles Times*, February 16, 1911). By the end of 1911 the Linton concessions had shipped 60 tons of abalone shells, and had beds of 3000 abalones that were used to grow abalone pearls. On December 9, 1911, the *Los Angeles Times* reported "The process is new, pearls being developed in the course of one or two years around a composition nucleus that is planted inside the abalone shell. Some of these have been removed from abalones after being planted eight months, and show the scheme is a success…"

Over the next year, however, Linton began to voice frustration over the number of abalone at the

Figure 9. Linton's Camp Number 6, San Nicolas Island, 1909.

islands being harvested commercially, as he lacked legal authority to stop anyone from taking his mariculture gastropods. Always on the lookout for economic opportunity, in April 1912 Linton took a four-month break and outfitted *Flyer* for an expedition to lower California in search of a reported 10 northern elephant seals (*Mirounga angustirostris*), thought at the time to be the last to exist, and each with an estimated value of $5000 (Sanford 1979). In addition to Linton, members of the expedition included Captain George H. Child; George Willett, ornithologist; H.N. Lowe, marine scientist; William McCluskey of the State Museum of Los Angeles; Ralph Johnson; Edward Bellringer; and Paul McCreary (*Los Angeles Times*, April 5, 1912). No log of the trip has been found; however, photographs of elephant seals taken on the voyage are on file at the Santa Cruz Island Foundation.

Upon *Flyer*'s return, Linton traveled to Washington, D.C. in July 1912 and met with officials from the U.S. Bureau of Fisheries to discuss the possibilities of establishing a preserve on one or more of the islands for "the study and advancement of the pearl-growing industry which

Figure 10. Linton's Japanese abalone divers.

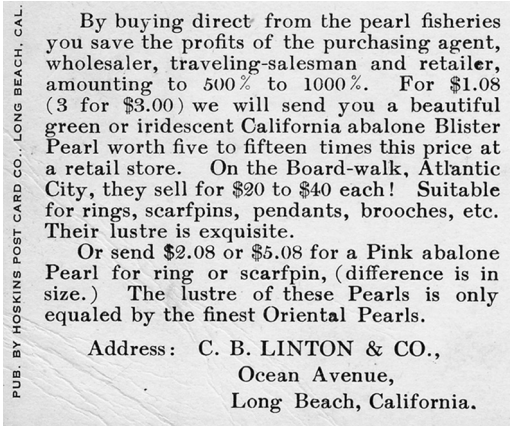
Figure 11. Linton's Japanese abalone harvesters.

has made considerable progress under private experiments" (*Los Angeles Times*, July 18, 1912). As commercial abalone harvesting continued, Linton's frustrations grew:

> Islands denuded. Clarence B. Linton of Long Beach, who has the abalone concession on San Nicolas and San Clemente Islands, says that "the accessible parts of the Channel Islands have been almost denuded of abalones, and that it will not be a very long while until the abalone shell and meat industry in Southern California will be a thing of the past..." (*Los Angeles Times*, August 27, 1912).

In February 1913, the government granted Linton a lease giving him exclusive rights to 12½ miles of San Nicolas Island coastline, both below high tide line and for a specified distance shoreward,

Figure 12. Abalone meat drying and abalone shells sacked for shipment to market.


By buying direct from the pearl fisheries you save the profits of the purchasing agent, wholesaler, traveling-salesman and retailer, amounting to 500% to 1000%. For $1.08 (3 for $3.00) we will send you a beautiful green or iridescent California abalone Blister Pearl worth five to fifteen times this price at a retail store. On the Board-walk, Atlantic City, they sell for $20 to $40 each! Suitable for rings, scarfpins, pendants, brooches, etc. Their lustre is exquisite.

Or send $2.08 or $5.08 for a Pink abalone Pearl for ring or scarfpin, (difference is in size.) The lustre of these Pearls is only equaled by the finest Oriental Pearls.

Address: C. B. LINTON & CO.,
Ocean Avenue,
Long Beach, California.

PUB. BY HOSKINS POST CARD CO., LONG BEACH, CAL.

Figure 13. Linton's post-card advertisement for his pearling operation on the islands.

for the propagation of pearls in abalones. With such a lease, Linton gained legal authority to punish those who would harvest his pearl mariculture beds (*Los Angeles Times*, February 28, 1913).

After six years of moderate success in the pearl mariculture business at various Channel Islands, and despite his success in obtaining a special coastal lease on San Nicolas Island in 1913, Linton gave up the mariculture business in 1914 and sold his boat *Flyer* to Channel Islands fisherman Charles Hanson (*Los Angeles Times*, May 23, 1914). Charles Brockman Linton set his place in history as California's pioneer mariculturist.

CONCLUSIONS

Clarence Brockman Linton was a Channel Islands entrepreneur, who between 1907 and 1910 collected and sold birds from the Channel Islands to museums and private collectors throughout North America and Europe. Linton's greatest contribution relative to the Channel Islands was as an amateur ornithologist. As a result of his bird collecting, Linton contributed a significant proportion of the Channel Islands bird specimens found in museum collections today. His publications documented the distribution and status of birds on San Clemente and Santa Cruz islands in the early 1900s. The birds that Linton collected from the islands serve as a temporal sample of material that can be used for future studies that require specimens from earlier time periods. Linton's specimens are also important because they can provide tissue samples that can be used for future genetic studies focused on the evolution and conservation of Channel Islands birds. Linton's work collecting birds on the islands has clearly added to the body of knowledge about the birds of the California Channel Islands and has provided specimens and important information relative to the distribution and status of birds on these islands during the early part of the twentieth century. In 1909, motivated by his discovery of a number of large pearls found in an archaeological site on San Nicolas Island, Linton became California's pioneer mariculturist when he developed the first pearl-growing industry in abalone beds around the California Channel Islands.

Figure 14. Linton purchased the 60-foot launch *Flyer* in September 1911 to service his island abalone harvest and mariculture interests.

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Appendix A . Birds collected by Clarence Brockman Linton on the Channel Islands from 1907 through 1910. SCRI = Santa Cruz Island, SNI = San Nicolas Island, SBI = Santa Barbara Island, SCLI = San Clemente Island

Scientific name	Common name	Endemic sub-species	SCRI	SNI	SBI	SCLI	Total collected
Accipiter striatus	Sharp-shinned hawk					1	1
Actitis macularia	Spotted sandpiper					1	1
Aeronautes saxatalis	White-throated swift		2				2
Aimophila ruficeps	Rufous-crowned sparrow	obscura	21				21
Amphispiza belli	Sage sparrow	clementeae				24	24
Anthus rubescens	American pipit					1	1
Aphelocoma insularis	Island scrub-jay	insularis	72				72
Aphriza virgata	Surfbird			1			1
Arenaria interpres	Ruddy turnstone			19			19
Arenaria melano-cephala	Black turnstone		12	6		5	23
Asio otus	Long-eared owl					1	1
Athene cunicularia	Burrowing owl		2	2		8	12
Calidris alba	Sanderling					2	2
Calidris minutilla	Least sandpiper			2		2	4
Calypte anna	Anna's humming-bird		5				5
Carduelis psaltria	Lesser goldfinch		1				1
Carpodacus mexicanus	House finch	clementis	20	3		24	47
Carpodacus purpureus	Purple finch		1				1
Catharus guttatus	Hermit thrush		4	1		26	31
Catharus ustulatus	Swainson's thrush					2	2
Catherpes mexicanus	Canyon wren		1				1
Cerorhinca monocerata	Rhinoceros auklet		9			2	11
Ceryle alcyon	Belted kingfisher					2	2
Charadrius alexandrinus	Snowy plover			2			2
Chondestes grammacus	Lark sparrow		1				1
Coccyzus americanus	Yellow-billed cuckoo		2				2

Appendix A (continued). Birds collected by Clarence Brockman Linton on the Channel Islands from 1907 through 1910. SCRI = Santa Cruz Island, SNI = San Nicolas Island, SBI = Santa Barbara Island, SCLI = San Clemente Island

Scientific name	Common name	Endemic sub-species	SCRI	SNI	SBI	SCLI	Total collected
Colaptes auratus	Northern flicker		4	1		3	8
Corvus corax	Common raven		9	1		5	15
Dendroica coronata	Yellow-rumped warbler					3	3
Dendroica petechia	Yellow warbler		3				3
Dendroica townsendi	Townsend's warbler		2			1	3
Empidonax difficilis	Pacific-slope flycatcher	insulicola	7			4	11
Empidonax traillii	Willow flycatcher		2	1		1	4
Eremophila alpestris	Horned lark	insularis	11	1		79	91
Euphagus carolinus	Rusty blackbird					1	1
Falco sparverius	American kestrel		2			2	4
Fulmarus glacialis	Northern fulmar		10				10
Gavia pacifica	Pacific loon		8				8
Gavia stellata	Red-throated loon		1				1
Haematopus bachmani	Black oyster-catcher		5				5
Haliaeetus leucocephalus	Bald eagle					1	1
Heteroscelus incanus	Wandering tattler		8	18	2	11	39
Icteria virens	Yellow-breasted chat		2				2
Ixoreus naevius	Varied thrush					4	4
Junco hyemalis	Dark-eyed junco		9			1	10
Lanius ludovicianus	Loggerhead shrike	anthonyi, mearnsi	11			11	22
Larus californicus	California gull			1		1	2
Larus heermanni	Heermann's gull		13	2		6	21
Larus occidentalis	Western gull			1		2	3
Melanitta perspicillata	Surf scoter		1				1
Melospiza lincolnii	Lincoln's sparrow		7				7
Melospiza melodia	Song sparrow	clementae, graminea			8	94	102

Appendix A (continued). Birds collected by Clarence Brockman Linton on the Channel Islands from 1907 through 1910. SCRI = Santa Cruz Island, SNI = San Nicolas Island, SBI = Santa Barbara Island, SCLI = San Clemente Island

Scientific name	Common name	Endemic sub-species	SCRI	SNI	SBI	SCLI	Total collected
Mergus serrator	Red-breasted merganser		1				1
Mimus polyglottos	Northern mockingbird		3			2	5
Numenius phaeopus	Whimbrel		3				3
Pandion haliaetus	Osprey					2	2
Passerculus sandwichensis	Savannah sparrow		3	2			5
Passerella iliaca	Fox sparrow		9			7	16
Pelecanus occidentalis	Brown pelican					1	1
Phalacrocorax auritus	Double-crested cormorant					3	3
Phalacrocorax penicillatus	Brandt's cormorant		1			8	9
Phalaropus fulicaria	Red phalarope		10				10
Phalaropus lobatus	Red-necked phalarope		1				1
Phoebastria immutabilis	Laysan albatross			1			1
Pipilo maculatus	Spotted towhee	clementae	27			71	98
Piranga ludoviciana	Western tanager		1			2	3
Piranga rubra	Summer tanager					1	1
Podiceps auritus	Horned grebe					1	1
Podiceps nigricollis	Eared grebe		3			3	6
Polioptila caerulea	Blue-gray gnatcatcher		2				2
Psaltriparus minimus	Bushtit		2				2
Ptychoramphus aleuticus	Cassin's auklet		3		2	2	7
Puffinus griseus	Sooty shearwater		1				1
Regulus satrapa	Golden-crowned kinglet		2				2
Salpinctes obsoletus	Rock wren		9	14		14	37
Sayornis nigricans	Black phoebe		2			2	4
Sayornis saya	Say's phoebe		1	1		3	5

Appendix A (continued). Birds collected by Clarence Brockman Linton on the Channel Islands from 1907 through 1910. SCRI = Santa Cruz Island, SNI = San Nicolas Island, SBI = Santa Barbara Island, SCLI = San Clemente Island

Scientific name	Common name	Endemic sub-species	SCRI	SNI	SBI	SCLI	Total collected
Selasphorus sasin	Allen's humming-bird	sedentarius	4			5	9
Sialia currucoides	Mountain bluebird					1	1
Sitta canadensis	Red-breasted nuthatch		3				3
Sphyrapicus nuchalis	Red-naped sapsucker					2	2
Spizella atrogularis	Black-chinned sparrow					1	1
Sturnella neglecta	Western meadowlark				1	1	2
Synthliboramphus antiquus	Ancient murrelet		2		2	2	6
Thalasseus maximus	Royal tern		1	1		11	13
Thryomanes bewickii	Bewick's wren	nesophilus, leucophrys	24			35	59
Troglodytes troglodytes	Winter wren		1				1
Tyrannus verticalis	Western kingbird					1	1
Tyrannus vociferans	Cassin's kingbird					1	1
Vermivora celata	Orange-crowned warbler	sordida	24			9	33
Vireo cassinii	Cassin's vireo		1				1
Vireo gilvus	Warbling vireo			1			1
Vireo huttoni	Hutton's vireo		24				24
Wilsonia pusilla	Wilson's warbler		2				2
Zenaida macroura	Mourning dove					1	1
Zonotrichia atricapilla	Golden-crowned sparrow		2				2
Zonotrichia querula	Harris' sparrow					1	1
		No. Specimens	440	82	15	524	1061
		No. Endemic Specimens	221 (50.2%)	4 (4.9%)	8 (53.3%)	356 (67.9%)	589 (55.5%)

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THE MOBILE REEF PROGRAM: A VEHICLE FOR SCIENCE LITERACY

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Abstract—The Santa Barbara Channel is a productive and diverse ecosystem that provides a rich resource for teaching toward science and environmental literacy. However, even though 98% of Santa Barbara and Ventura county schools lie within 15 miles of an accessible beach, close to 70% of the area's students had never been to the beach and knew very little, if anything, about the Channel Islands. Moreover, in recent years, there has been an alarming, downward trend in outdoor and informal science educational experiences. To address these concerns we used a mobile marine laboratory and pre- and post-classroom visit assessments to increase science literacy in local schools. By using a pre-visit assessment to determine levels of student knowledge of water, watersheds, and human impacts in watersheds, the Mobile Research Experience and Education Facility (REEF) Program was able to visit a class with the tools to address the identified weaknesses. Using touch tank aquaria and digital globe technology, students were taught specific science concepts related to state standards. Students then received a field trip to an educational aquarium. This had a twofold outcome. First, students were better informed prior to their "outdoor" experience. Second, having some pre-trip exposure to marine organisms enabled "first-time" visitors to the aquarium to have greater focus and improved learning. Comparison of pre- and post-assessment scores from 425 elementary and middle school students at five Ventura and Santa Barbara county schools showed a 22% increase in the understanding of the science concepts taught.

INTRODUCTION

Science is hands-on. It is messy, it begs questions, creates dialogue, uses math, is rich in history, and has an immense impact on society. And yet, as a society, our knowledge of science is lacking (NSF 2001). Furthermore, compelling arguments have been made that one cannot be science-literate without being ocean-literate (Strang et al. 2007). It would seem reasonable, then, that coastal communities should be more ocean-literate, based on proximity alone. Yet, in 2003, the Pew Ocean Commission reported the need to improve public literacy about oceans (Pew Charitable Trusts 2003). A 2005 poll of over 1200 individuals from coastal and non-coastal states revealed little difference in self-assessed level of knowledge with ocean and coastal policy issues (Steel et al. 2005). Another poll of 1106 citizens revealed a similar trend with regard to familiarity with terms and concepts associated with coastal and ocean management issues (Steel et al. 2005). Whereas approximately 50% of the respondents said they were somewhat informed with regard to ocean and coastal policy issues, only 10% said they were informed and 4% very well informed.

Santa Barbara and Ventura counties combined have four community colleges, two private colleges, one California State University, and one University of California campus. The two counties share a number of national parks and national forests, the Santa Barbara Channel Islands National Marine Sanctuary, as well as over 100 state and regional parks. They both have a number of major watersheds. Ninety-eight percent of the 255 schools in Santa Barbara and Ventura counties lie within 15 miles of an accessible beach. One would think, given the rich and diverse environment associated with the Santa Barbara Channel Islands, that science literacy, especially with relation to marine science, would not be an issue with regards to K-12 education. Yet, at many elementary schools in Santa Barbara and Ventura counties, science is all but absent in the classroom.

Exacerbating this apparent disconnect is a downward trend in visits by California school groups to institutions supporting informal science education. In an e-mail, which circulated amongst

marine educators on the listserv *OceanList*, feedback from teachers and informal educators around the country indicated that many other institutions were also experiencing a decline in school group attendance. Reasons for the decline fell into four categories: administrative, financial, staffing, and academic focus. We believe these factors could be further reduced, and potentially linked, to economics and/or academics.

The Marine Science Institute (MSI) at the University of California, Santa Barbara has developed one method for delivering effective, informal science education curriculum. For the past two decades the MSI has run a successful informal touch tank program serving approximately 5000 K–12 students annually. In the fall of 2004, MSI opened the Research Experience & Education Facility, also known as the REEF. The REEF is a teaching aquarium facility that serves as an informal science center for K–16 students and the general public in Santa Barbara and Ventura counties. Shortly after opening, REEF experienced a decline in visitation that echoed the findings discussed on *OceanList*, with many schools from Ventura County canceling their visits citing budget woes and the war in Iraq (Ventura has a number of military bases) as reasons for canceling.

The Mobile REEF, designed to fill the needs of schools that could not afford to visit the REEF, utilizes portable touch tanks and curriculum based on California State Science Standards to take marine science into classrooms. Through collaboration with the Santa Barbara Museum of Natural History Ty Warner Sea Center, a specially designed van was outfitted with the MSI Mobile REEF touch tanks, a 14" Magic Planet® from Global Imagination, and curriculum based on state standards and assessment tools modified from Kellogg Biological Station's Environmental Literacy Project to evaluate the outcomes of this project. Here we report how pre- and post-classroom assessment enabled us to address specific knowledge gaps and evaluate the effectiveness of classroom visits.

MATERIALS AND METHODS

Through classroom hands-on activities and inquiry-based questioning strategies, the Mobile REEF utilizes touch tanks and the Magic Planet® to

Table 1. Mobile REEF Program pre/post test questions adapted from Kellogg Biological Station's Environmental Literacy Project.

Question number	Questions presented to the students	Options
1	About what percentage of the Earth's surface is covered with water?	A. 30%; B. 55%; C. 75%; D. 90%
2	About what percentage of the water on Earth is fresh water?	A. 1%; B. 3%; C. 12%; D. 20%
3	Where is most of the fresh water on the Earth found?	Students list answers
4	What form is most of the fresh water on the Earth found?	Students list answers
5	Where do you think the water in the clouds comes from, and how does it get there?	Short answer
6	What are some factors that animals in a wetland have to adapt to?	Students list answers
7	Draw in mountains that act as watershed boundaries on the map below	Student provided with a diagram of rivers with tributaries draining into an ocean.
8	If a water pollutant is put into the river at town C, which towns (if any) would be affected by the pollution?	Based on diagram in Q7 with points A, B, C, D
9	Explain why only these towns would be affected.	Short answer

teach and assess students' grasp of California State Science Standards for grades 4–8. The program is designed to take place during a one-class period, which ranges in time from 50–65 minutes. Students are divided into two groups. Each group spends ~20 minutes at the touch tanks and 20 minutes at the Magic Planet® followed by a 10-minute summary. Assessments were administered to students by their teachers before and after the Mobile REEF visits to track the effectiveness of the program, and to identify misconceptions about watershed science that could be addressed during the classroom visit. Thus, specific topics covered in the classroom visit are determined by analysis of pre-assessment testing results. Assessment questions ranged from percent of planet covered in water, to an understanding of adaptations to wetland habitats (Table 1).

Touch Tanks

The Mobile REEF utilizes two, specially designed, 45-gallon (170 L) touch tanks with recirculation pumps and chillers to hold and exhibit local marine organisms. Students are first encouraged to handle and observe the various organisms. This is followed with a brief discussion, using graphics, to illustrate characteristics of the organisms' habitat(s). Students are then asked, based on grade level, to group the organisms based on morphology, adaptations to abiotic and biotic factors, or ecology. Students must support their conclusions with evidence gained during their observations and knowledge about the organisms' habitats.

The Magic Planet®

The topics for questions 1–4 were addressed, in class, utilizing the Magic Planet®, which gives students a 3-dimensional view of the planet accompanied by a diagrammatic review of the water cycle and development of hypothesis and visualization, based on real data, on the Magic Planet®. The digital projection globe contains visualized, moving, satellite imagery from astronomical, tectonic, and meteorological data supplied by NASA, NOAA, and others. First, based on pre-assessment results and through the use of a guided discussion using a chalkboard or dry eraseboard, students' knowledge of the water cycle and watersheds is assessed. Staff then use the globe's meteorological data with continued guided discussions to show the relationship between the water cycle and major geophysical features. Students are asked to develop hypotheses about where they might expect more/less precipitation and to support their hypotheses based on discussions. This is followed by a wrap-up discussion of the Earth's biomes and climate and the role that ocean circulation patterns play.

Following the activities at the touch tanks and the globe, students are led in an open-ended discussion based on each particular class' experience with the Mobile REEF unit. The discussion allows staff to address any persisting misunderstandings and/or misconceptions revealed in the pre-assessment or during the activities. Following the classroom visit, teachers administer the post-assessment to students, and the results are forwarded to Mobile REEF staff.

The Mobile REEF van visited 12 elementary schools, 4 middle/junior high schools, and 3 high schools in Santa Barbara and Ventura counties in 2006–2007. Post-assessment scores were compared to pre-assessment scores for 425 G4–8 students at 5 of the 12 schools visited.

RESULTS

Comparison of pre- and post-classroom visit assessments showed that student understanding improved for 7 of the 9 questions (Fig. 1). After the lesson, the understanding of where and in what form water is found improved by at least 20% (questions 1–4). The question regarding the source of water in clouds (question 5) showed no significant change between pre- and post-testing (>80% for both periods), and correct responses for the question regarding adaptation of wetland species (question 6) decreased by 17% between testing periods. The latter was the only question on which student understanding decreased after the classroom visit. A dramatic increase in understanding of watersheds (questions 7–9) was apparent after the lesson. Prior to visits, less than 17% could correctly draw the boundaries of a watershed (question 7), whereas after a visit approximately 66% were able to do so. Responses to both questions regarding routes of

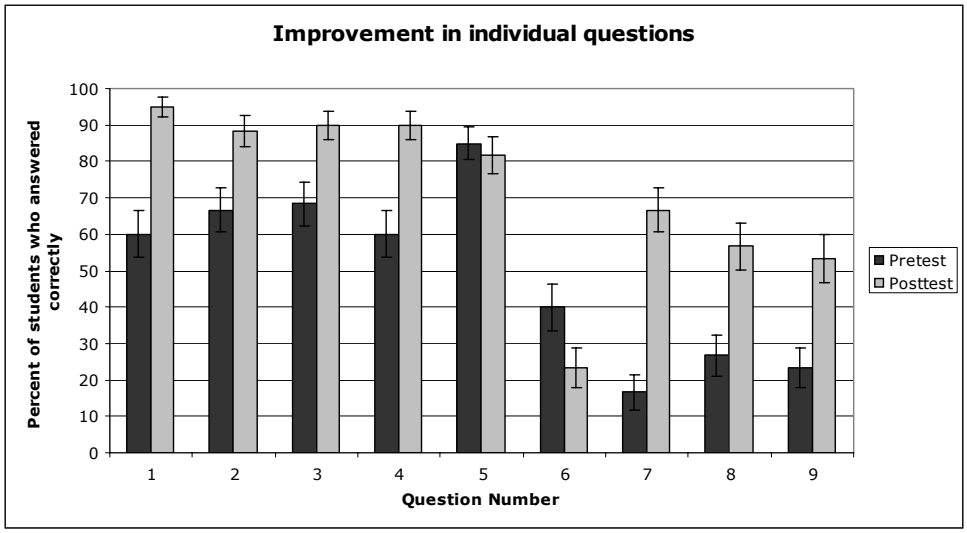

Figure 1. Change in percent correct responses, by question, between the Mobile REEF Program pre-test and post-test evaluation. Bars show mean correct responses with error bars. Questions are found in Table 1.

pollution (questions 8 and 9) improved by 30% between evaluations.

DISCUSSION

Incorporating pre- and post-classroom visit assessment showed that the Mobile REEF program improved student knowledge about key concepts, and facilitated the educational experience by allowing educators to address knowledge gaps. In this respect the Mobile REEF program serves as a model for other off-site environmental education programs, which could both increase and document their effectiveness by incorporation of such assessments.

It is instructive to examine the specific questions on which student performance did not improve. There was no significant change in the number of students correctly answering question 5, which assessed students' grasp of the water cycle by asking them to explain the origin of clouds. The lack of change could possibly be due to the difference between a slight variation in the pre- and post-assessment questions. Question 6, regarding wetland animals and their adaptations, was answered correctly by 17% fewer students after the classroom visit, and performance was low both pre- (40%) and post-classroom visit (23%). Students may have confused wetland animals with the rocky intertidal animals they saw in the touch tanks. Moreover, through diagnostic assessment it was determined that students that took the test prior to the lesson did not understand the diagram associated with questions 7–9. The dramatic improvement in those questions is attributed to the in-class lesson utilizing inquiry and guided discussion with students to re-create a similar diagram.

While the Mobile REEF was designed to teach to specific state standards, one of the most valuable lessons learned was what students in specific grades really know about topics in science, how they have arrived at that knowledge, and how to adapt the program *in situ* to respond to a specific groups understanding. For example, questions 7, 8, and 9 refer to mountains, urban development, and watersheds. Santa Barbara and Ventura are characterized by their Mediterranean climate. It has been assumed that, given our proximity to the ocean and mountains and the amount of urban development, students have a basic understanding of the ecosystem processes associated with the region. Theoretically, this should be further developed and supported by the high number of environmental organizations addressing watershed pollution. However, pre-assessment responses showed the contrary. During our visits, when students were given a drawing of our region, with mountains, lakes, rivers, urban development, and ocean, and asked to define a watershed, most

pointed to farm buildings, or stated that a watershed was a room ("shed") in which water was kept. Whereas hands-on classroom science experiences offered by programs such as Mobile REEF have a demonstrably positive impact on students' understanding of science topics, it is also clear that further research is necessary to develop assessments that get at the core of science curriculum literacy.

Finally, although only anecdotal at this point, staff from related programs (MERITO, LiMPETS, Ty Warner Sea Center, and the REEF) all have related that students exposed to the Mobile REEF Program were better prepared for the questions presented to them. It was further noted that students were more focused on topics and less affected by peripheral distractions (plant/animal movement/ contact, waves, etc.) associated with field experiences. This allows for these types of experiences to be truly educational, as opposed to "edutainment."

While it cannot address every misunderstanding and misconception, the Mobile REEF serves as a good model for supporting school science curriculum. The program's success extends to its ability to get students thinking in a logical, scientific manner, which prepares them for future hands-on experiences and other situations in which critical thinking is required. This approach could also be used to close other obvious gaps in student understanding on other critical science issues, such as the rate, scope, and impact of global climate change. Implementing methods to bring hands-on experiences to students at a time when schools are limiting off-campus activities is a major step toward maintaining high quality science education.

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VARIATION IN STABLE CARBON AND NITROGEN ISOTOPE VALUES FROM MULTIPLE TISSUES OF CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*)

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Abstract—Stable nitrogen and carbon isotope analyses have increasingly been used to investigate the foraging ecology of marine mammals, particularly in response to the limitations of using conventional dietary analysis techniques. In this study, we compared nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values of four different tissues (i.e., fur, red blood cells, serum, and plasma) from California sea lions (*Zalophus californianus*; n = 58) of various age classes (i.e., pup, yearling, juvenile, and adult). Metabolically active tissues with relatively high turnover rates (plasma and serum) had similar $\delta^{15}N$ and $\delta^{13}C$ values, but these two tissues had significantly higher $\delta^{15}N$ values and lower $\delta^{13}C$ values in comparison to red blood cells or fur. In general, $\delta^{15}N$ values decreased with increasing age; $\delta^{15}N$ values for pups were between 1.2‰ (fur) to 2.0‰ (serum) greater in comparison to adult females. In general, $\delta^{13}C$ values increased with age (except red blood cells). Pups had mean $\delta^{13}C$ values that were 0.4‰ (plasma) to 0.5‰ (fur and serum) lower than mean values of adult females. Stable isotope analysis of various tissues can provide dietary information at the individual level on different temporal and spatial scales, as well as reveal patterns of the foraging ecology among groups of animals.

INTRODUCTION

The limitations and biases of using traditional methods to examine the diet of pinnipeds (e.g., analysis of stomach contents of harvested or recently dead individuals, stomach lavage, regurgitations, fecal analysis, and direct observation) have been well documented (Jobling and Breiby 1986; Jobling 1987; Dellinger and Trillmich 1988; Harvey 1989; Gales and Cheal 1992; Harvey and Antonelis 1994; Cottrell et al. 1996; Tollit et al. 1997; Bowen 2000; Orr and Harvey 2001; Arim and Naya 2003; Gudmundson et al. 2006). A noteworthy limitation of these methods is that each analysis represents only a "snapshot" of prey consumed prior to collection (Hobson et al. 1997). Although fecal samples, which are now routinely collected to assess the diet of pinnipeds, provide information about dietary composition, they do not provide information about the age or sex of the consumer; therefore, dietary changes within individual or intraspecific comparisons are not possible. Biochemical methods (e.g., serology, fatty acid signature analysis, and stable isotope analysis) have been developed to overcome some of the problems associated with using conventional techniques (e.g., Hobson 1990; Wada et al. 1991; Iverson et al. 1995; Kirsch et al. 2000). Stable isotope analysis (SIA) is based on the idea that the stable isotope composition of a consumer's diet is reflected in its tissues. Because different tissues have dissimilar isotopic turnover rates, an isotopic approach can provide time-integrated data on average dietary intake, rather than a recent "snapshot" of information derived from traditional proxies (Kirsch et al. 2000).

The analysis of naturally occurring stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) is now frequently used to investigate changes in feeding patterns and habitat utilization of animals in space and time (Hobson et al. 1996; Das et al. 2003; Dalerum and Angerbjörn 2005; Sinisalo et al. 2008). Due to the preferential excretion of ^{14}N in urine, $\delta^{15}N$ values increase by ~3–5% per trophic level in marine food webs (DeNiro and Epstein 1978; Minagawa and Wada 1984; Owens 1987;

Wada et al. 1991; Hobson and Welch 1992; Vander Zanden and Rasmussen 2001; Kurle 2002). Therefore, the relative amount of ^{15}N in tissues reflects the trophic level at which the consumer is feeding, with higher $\delta^{15}N$ values corresponding to higher trophic levels. The ratio of stable carbon isotopes varies little with trophic position. Only ~0.5–1.1‰ enrichment per trophic level has been observed for $\delta^{13}C$ values in marine food webs (e.g., Fry and Sherr 1984; Wada et al. 1991; Kurle 2002). However, $\delta^{13}C$ values are affected by factors that act at the base of the food web, such as phytoplankton size and growth rate (Schoeninger and DeNiro 1984; Laws et al. 1995; Bidigare et al. 1997), resulting in geographic differences in $\delta^{13}C$ values that can be used to indicate consumer foraging locations ($\delta^{13}C$ enrichment: fresh water > marine, nearshore > offshore, benthic > pelagic; Rau et al. 1982; Rau et al. 1983; Fry and Sherr 1984; Wada et al. 1991; France 1995; Hobson et al. 1997; Burton and Koch 1999). For example, primary producers in nearshore/benthic areas are relatively more ^{13}C enriched compared to those in offshore/pelagic regions where nutrients are relatively limited, phytoplankton growth rates are lower, and the base of the food web is more enriched in ^{12}C (Fry and Wainright 1991; France 1995; Pancost et al. 1997).

Although the isotopic composition of an animal is determined by its diet, there is substantial isotopic variation among tissues. Isotopic signatures assessed from consumer tissues with high turnover rates (e.g., blood plasma, liver) reflect recent dietary intake, whereas tissues with slower turnover rates (e.g., muscle, bone collagen) reflect feeding over a longer period of time (Tieszen et al. 1983). This is a result of nutrients of tissues being assimilated at time scales dependent upon the metabolism and protein turnover rate of a particular tissue (Kurle and Worthy 2002; Dalerum and Angerbjörn 2005). Because different tissues equilibrate to dietary isotopic changes at different rates, it should be possible to examine the diet of a consumer over multiple temporal scales by examining the isotopic composition of multiple tissues (Phillips and Eldridge 2006).

Stable isotopes have been used to describe the foraging ecology of several pinniped species (e.g., Hobson et al. 1996, 1997; Hobson and Sease 1998; Burton and Koch 1999; Kurle 2002; Newsome et al. 2006; Zhao et al. 2006; Sinisalo et al. 2008); however, few studies have utilized multiple tissues with dissimilar turnover rates collected from wild populations. Here, we did not compare sea lion isotope values to those of their prey, which is necessary to provide more direct information about trophic level or foraging location. Instead, we examined the pattern of variation in nitrogen and carbon isotope values within individuals and among different age classes of California sea lions (*Zalophus californianus*) to establish the use of SIA as a useful tool for the study of temporal diet shifts within and among individual sea lions.

MATERIALS AND METHODS

Field Collection

California sea lion tissues were collected from individuals at San Miguel Island, California (SMI; 34.03°N, 120.44°W), during 2006 and 2007. The animals were captured as part of ongoing studies conducted by the National Marine Fisheries Service's National Marine Mammal Laboratory at SMI, which supports one of the two largest *Zalophus californianus* rookeries in the world. Tissues collected were fur, red blood cells (RBCs), plasma, and serum. The growth rate of fur is slower than turnover rates for blood components (i.e., metabolically active tissues), and RBCs have slower turnover rates than serum or plasma (Tieszen et al. 1983; Hobson and Clark 1993; Hilderbrand et al. 1996; Klaassen et al. 2004). Therefore, the isotopic measurement of fur should provide long-term dietary information reflecting integration over several months. For animals that undergo an annual molting cycle like all otariids (assuming the entire shaft was collected and completely homogenized), the isotopic signature of fur will reflect diet since the previous molt. For pinnipeds, plasma and serum have high turnover rates and are likely to provide dietary information from 1 to 2 weeks prior to collection (Kurle 2002), whereas RBCs are likely to represent the average isotopic composition of diet integrated over two or more months (Kurle 2002; Zhao et al. 2006).

Samples of all four tissues were obtained from 58 individuals (Table 1). Fur was obtained by cutting an ~2 cm x 2 cm patch near the dorsal rump region of each animal using electric clippers or

Table 1. Mean $\delta^{15}N$ and $\delta^{13}C$ values of tissues collected from California sea lions of various age classes that were captured and sampled at San Miguel Island, California, during September 2006 through January 2007. Values in parentheses indicate standard error.

Age Class	Fur		RBC		Serum		Plasma	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Pup (< 1 yr; n = 39)	18.4 (0.1)	-13.9 (0.1)	18.4 (0.1)	-14.9 (0.0)	19.3 (0.1)	-15.4 (0.0)	19.4 (0.1)	-15.3 (0.0)
Yearling (1 - 2 yr; n = 3)	18.1 (0.1)	-13.6 (0.1)	17.0 (0.1)	-15.3 (0.1)	17.9 (0.1)	-14.9 (0.3)	17.7 (0.1)	-15.0 (0.4)
Juvenile (2 - 4 yr; n = 9)	17.2 (0.1)	-13.5 (0.1)	16.7 (0.0)	-15.3 (0.0)	17.9 (0.1)	-15.1 (0.1)	17.8 (0.1)	-15.1 (0.1)
Adult (≥4 yr; n = 7)	17.2 (0.2)	-13.4 (0.2)	16.5 (0.1)	-15.2 (0.1)	17.4 (0.0)	-14.9 (0.1)	17.6 (0.3)	-14.9 (0.1)

scissors applied to the base of the fur without removing the follicle. Samples were stored dry in envelopes until further processing in the laboratory. Blood samples were obtained during routine collections from the caudal-gluteal vein. Plasma and RBCs were collected in tubes containing the anticlotting agent sodium heparin, which has been determined not to alter isotopic values (Hobson et al. 1997; Kurle 2002). Serum was collected from tubes containing a clot activator for serum separation, also known not to cause isotopic alterations (Kurle 2002). Blood components were obtained after 10 min of centrifugation. Approximately 1 mL of each component was decanted into a 2 mL cryovial and frozen at -40°C until further processing.

Stable Isotope and Statistical Analyses

Once in the laboratory, fur samples were placed in scintillation vials and cleaned by washing them with a mild detergent solution, followed by a rinse with de-ionized (DI) water. Surface contaminants were removed using a solvent wash (2:1 chloroform:methanol) and another DI water rinse. Samples were then placed in a lyophilizer and dried for 24 to 48 h. Frozen blood samples also were placed into the lyophilizer. Once dried, all samples were powdered and homogenized using a mortar and pestle (fur) or glass rod (blood components). Samples were weighed into tin capsules (8 x 5 mm) to a target weight of 1.0 ± 0.2 mg.

Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values of all tissues analyzed in this study were determined using a Carlo-Erba elemental analyzer (NC 2500)[1] interfaced with a Finnegan Delta Plus XL[1] mass spectrometer in the light stable isotope facility at Carnegie Institution of Washington (Washington, DC). Isotopic results are expressed in δ notation: $\delta^{15}N$ or $\delta^{13}C = 1000 * [(R_{sample}/R_{standard})-1]$, where R_{sample} and $R_{standard}$ are the $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratios of the sample and standard, respectively. The standards used were atmospheric N_2 for nitrogen or Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon. The units are expressed as parts per thousand or per mil (‰) and are calibrated to international standards through repeated measurements of an organic standard of known isotopic composition. The within-run standard deviation of an acetalinide standard was 0.2‰ for both $\delta^{15}N$ and $\delta^{13}C$ values.

Tissues within an individual were compared amongst each other using a blocked one-way analysis of variance (blocked ANOVA). Additionally, we used one-way ANOVAs to compare $\delta^{15}N$ or $\delta^{13}C$ values among age classes (i.e., pup (< 1 yr), yearling (1–2 yr), juvenile (2–4

1. References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

yr), and adult (≥ 4 yr)). When significant differences were detected, pairwise multiple comparisons were conducted using Tukey's Honest Significant Difference (HSD) method (Zar 1999). Significance was tested at the $\alpha = 0.05$ level. Statistical analyses were performed using R Program Language (ver. 2.4.1; R Development Core Team 2006).

RESULTS

Within Individual

The $\delta^{15}N$ and $\delta^{13}C$ values differed among sample types (blocked ANOVA: F = 172.96, df = 3, P < 0.001 for $\delta^{15}N$; and F = 340.61, df = 3; P < 0.001 for $\delta^{13}C$). Plasma and serum had higher (enriched) $\delta^{15}N$ and lower (depleted) $\delta^{13}C$ values compared to RBCs and fur (Fig. 1). Subsequent tests indicated that there were no significant differences between $\delta^{15}N$ or $\delta^{13}C$ values for plasma and serum (Tukey's HSD: P = 1.00 and 0.32, respectively), however significant differences remained between these two tissues and the others (Tukey's HSD: for all comparisons P < 0.002).

Among Age Classes

There were significant differences in mean $\delta^{15}N$ values among age classes. In general, $\delta^{15}N$ values decreased with increase in age (Table 1). Subsequent tests indicated that there were differences among all age combinations except between adult-juvenile and yearling-pup for fur (Tukey's HSD: 1.00 and 0.67, respectively; all other comparisons $P < 0.007$; Table 1). For the remaining tissues, only pups had significantly different mean $\delta^{15}N$ values compared to the other age classes (Tukey's HSD: for all comparisons $P < 0.001$; Table 1). The magnitude of difference of $\delta^{15}N$ values of pups and adult females was least for fur (1.2‰) compared to blood components (≥ 1.8‰).

There were no significant differences among age classes in mean $\delta^{13}C$ values for fur or plasma except between adult-pup and juvenile-pup (fur), and adult-pup (plasma), respectively (ANOVAs; for all comparisons $P < 0.008$). Pups had significantly higher mean RBC $\delta^{13}C$ values and significantly lower mean serum $\delta^{13}C$ values compared to all the other age classes (ANOVAs; for all comparisons $P < 0.02$). There were no significant differences in mean $\delta^{13}C$ values among older age classes (ANOVAs; for all comparisons $P > 0.52$; Table 1). The magnitude of difference of $\delta^{13}C$ values between pups and adult females was similar among all tissues (~ 0.5‰).

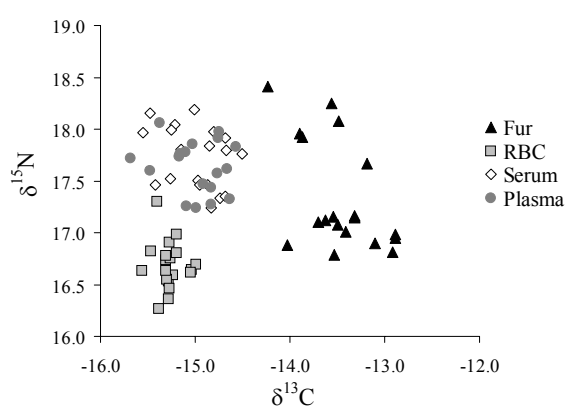

Figure 1. The relationship between $\delta^{13}C$ and $\delta^{15}N$ of different tissues sampled from California sea lions at San Miguel Island during 2006 and 2007. Pup values were excluded for clarity.

DISCUSSION

Stable isotope ratios in consumer tissues are useful for discerning dietary components assimilated over time; however, it is important to be mindful of the physiological, biochemical, and ecological factors that greatly influence the patterns of isotope values among tissue types and individuals (Gannes et al. 1997). Also noteworthy is that isotopic signatures determined at a given point in time do not reflect the current or the previous diet but are time-integrated products of both (Sweeting et al. 2005). Without pertinent information on turnover rates of tissues, isotopic signatures will only be loosely descriptive of diet (Gannes et al. 1997). In this study, we did not measure diet-tissue isotopic fractionations; however, we provided unique information about general isotopic patterns from multiple tissues from wild California sea lions of various age classes.

Within Individual

There were significant differences in isotope values among tissues within individuals. Besides being indicative of changes in dietary intake and trophic level at different time scales, discrepancies

in $\delta^{15}N$ values among tissues of an individual could have resulted from differences in the macromolecular composition (i.e., amino acids, lipids) of tissues (Kurle 2002; Zhao et al. 2006). Results from several studies on captive birds and mammals have indicated that isotope values of different tissues from the same individual do vary in a systematic way, even when the animal is fed an isotopically monotonous diet (Tieszen et al. 1983; Sutoh et al. 1987; Hobson and Clark 1993; Hobson et al. 1996; Kurle 2002; Vanderklift and Ponsard 2003; De Smet et al. 2004; Sponheimer et al. 2006; Zhao et al. 2006). $\delta^{15}N$ values of plasma and serum were similar to each other and more enriched compared to RBCs and fur. These two tissues are similar except plasma contains fibrinogen and other clotting-factor proteins (Schier et al. 1996). Kurle (2002) stated that differences in amino acid composition likely explained differences in $\delta^{15}N$ values among blood constituents in captive northern fur seals (*Callorhinus ursinus*) that were fed an isotopically homogeneous diet throughout the study.

Overall, $\delta^{13}C$ values of fur were more enriched compared to the blood components; RBCs in turn were more enriched compared to serum and plasma. These findings were similar to previous studies of other pinniped species (Hobson et al. 1996, 1997; Kurle 2002; Zhao et al. 2006). As with stable nitrogen isotope values, discrepancies of $\delta^{13}C$ values among tissues of an individual could reflect temporal shifts in diet and/or habitat use or may relate to the differences in the amino acid composition or lipid content in the tissues (Kurle 2002; Zhao et al. 2006). For example, serum albumin is the major carrier of fatty acids in blood (Nelson 1970), and lipids are ^{13}C-depleted in comparison to associated proteins (Kelly 2000), which results in lower $\delta^{13}C$ values (Kurle 2002). Zhao (2002) noted that carbon and nitrogen isotope ratios differ greatly among individual amino acids. Therefore, the lipid and/or amino acid content present in blood could have been a contributing factor in the lower mean $\delta^{13}C$ values of the blood components in comparison to those of fur. Unlike captive animals, wild sea lions usually do not have an isotopically homogeneous diet, therefore changes in their diet (prey species, acquisition location) and tissue composition must be factored in explaining differences in $\delta^{15}N$ and $\delta^{13}C$ values among different tissues.

Among Age Classes

Significant differences in mean $\delta^{15}N$ and $\delta^{13}C$ also were observed among age classes. Our limited samples sizes for particular age classes (i.e., yearlings and adults) prohibit definitive conclusions, however interesting patterns persisted nonetheless. Pups had higher $\delta^{15}N$ values for all tissues compared to those of older animals. This was expected because most, if not all, of their diet is obtained from their mothers in the form of milk. Milk is derived from remobilized body tissues of lactating females. Because pups, in essence, were feeding on their mothers' tissues, they were feeding at a higher trophic level than older conspecifics. Yearlings had intermediate $\delta^{15}N$ values for fur and similar $\delta^{15}N$ values for blood components compared to those of older animals. As previously mentioned, fur can reflect integrated dietary information over several months (depending on when collected). Therefore, it is likely that the isotopic-composition of fur from yearlings partially reflected their pre-weaned milk diet, resulting in higher $\delta^{15}N$ values. However, their $\delta^{15}N$ values for plasma, serum, and RBC were not statistically different from those of juveniles and adults. Because the isotopic signatures of blood components reflect recent diet, this pattern indicates that yearlings were weaned at the time of sampling and were feeding at a similar trophic level as older individuals. Juvenile and adult sea lions had similar $\delta^{15}N$ values for all tissues, indicating that they were feeding at approximately the same trophic level. There were greater magnitudes of difference in $\delta^{15}N$ values of blood components compared to those of fur between pups and juveniles/adults. This exemplifies that the choice of tissue(s) is important, particularly when assessing ontogenetic or other temporal shifts in diet.

In contrast to $\delta^{15}N$ values, pups had significantly lower $\delta^{13}C$ values than those of older age classes (except for RBCs); $\delta^{13}C$ values for yearlings, juveniles, and adults were statistically nonsignificant. The most likely reason for this pattern is that pups were still dependent on their mothers and were sustained on a lipid-rich milk diet, which is ^{13}C depleted in comparison to a relatively protein-rich piscivorous diet (Tieszen et al. 1983;

Tieszen and Boutton 1988; Polischuk et al. 2001; Kurle 2002). There was an opposite trend for RBCs, which might be due to their lower proportion of lipids in comparison to plasma and serum. The fact that individuals of older age classes had similar $\delta^{13}C$-values may indicate that they were feeding in similar areas. All of the non-pup animals sampled in this study were females. Findings from telemetry studies of different-aged females instrumented on San Miguel Island indicated that many of these animals feed on epi-pelagic prey in shallow waters (Feldkamp et al. 1989; Melin et al. 2008; Orr unpublished data).

In summary, examining the stable carbon and nitrogen isotopes from various tissues provides a better temporal understanding of the foraging ecology of a species compared to using conventional dietary proxies (e.g., fecal analysis) or isotopic data from a single tissue. The application of stable isotope analysis can be strengthened when used in conjunction with other techniques. For example, fecal analysis can be used to "ground truth" the use of isotopic proxies to assess the foraging ecology of a consumer at a particular location (Burns et al. 1998; Porras-Peters et al. 2008). The choice of tissue(s) to analyze will affect conclusions about a consumer's diet. SIA is very useful when researchers are interested in estimating the diet or the change therein of a particular individual or group of animals within an age or sex class over different time periods. Determining the diet of various age classes might be of special concern for those species whose status is dependent on juvenile survival. Using stable isotopes, researchers can determine when weaning occurs and ascertain differences in the foraging ecology of juveniles and adults. Also, SIA is useful when only a segment of the population is accessible for sampling. For example, it is often difficult to capture and collect tissue samples from large top consumers (e.g., adult female pinnipeds); however, it may be relatively easy to acquire samples from their small, dependent offspring. The diet and movement patterns of adult females can be indirectly determined by analyzing the tissues of their offspring after suitable isotopic fractionations are considered (Aurioles-Gamboa et al. 2006; Porras-Peters et al. 2008). It is vital to have an understanding of diet-consumer tissue isotopic fractionations so that proper interpretations and comparisons can be made within and among individuals, species, or projects.

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THE NATURAL HISTORY OF *UNDARIA PINNATIFIDA* AND *SARGASSUM FILICINUM* AT THE CALIFORNIA CHANNEL ISLANDS: NON-NATIVE SEAWEEDS WITH DIFFERENT INVASION STYLES

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Abstract—The new millennium ushered in two prominent non-native subtidal seaweeds to southern California: *Undaria pinnatifida* (Harvey) Suringar (Laminariales) and *Sargassum filicinum* Harvey (Fucales), both originally from Asia. Our long-term and widespread survey program provided the opportunity to document their establishment and dispersal at the Channel Islands. The two species exhibit very different invasion patterns. *Undaria* is well known for invading a broad spectrum of habitats throughout the world; however, California is the first region outside of Asia at which little-known *S. filicinum* has been reported. In 2001, *Undaria* was discovered at a single sheltered cove on the lee side of Santa Catalina Island, on a deep (24 m) soft sediment substrate. In subsequent years, it moved onto shallow subtidal rocky habitat, mixing with the *Macrocystis* kelp forest community. By 2004, it was well established at the primary site and was found at a second adjacent site. Surprisingly, our subsequent surveys at Santa Catalina Island and the other Channel Islands, as well as alerts to the diving community, have not yielded new populations, despite this species' aggressive spread in harbors on the mainland. In contrast, *S. filicinum* was initially discovered in the leeward Isthmus area at the western end of Santa Catalina Island in spring 2006. In one year, it spread rapidly along the entire lee side to Avalon, forming dense groves. In 2007, we documented this species on the windward side of Santa Catalina Island and discovered populations at two locations on the lee side of San Clemente Island. We expect *S. filicinum* to spread further at the Channel Islands and along the southern California mainland. We report the current distribution and compare the life histories of these two invasive species.

INTRODUCTION

Seaweeds that have been introduced by human activities to regions beyond their native range, where they establish and thrive, are considered invasive species. These invaders are a focus of concern because of their potential to compete with native species and alter community composition and dynamics. A total of 277 species of invasive seaweeds have been reported worldwide, most likely dispersed via hull-fouling and aquaculture, including shellfish farming (Williams and Smith 2007). Thirteen species of non-native seaweeds have been reported from California (Miller 2004; Miller et al. 2007), accounting for about 2% of the California seaweed flora.

Perhaps the most widespread and conspicuous of these is the brown seaweed *Sargassum muticum* (Yendo) Fensholt (Fucales). Originally from northeast Asia, *S. muticum* was first reported on the west coast of North America in the early twentieth century (Scagel 1956), reached southern California in 1970 (Setzer and Link 1971) and has become a common component of California intertidal and subtidal communities (Ambrose and Nelson 1982; Deysher and Norton 1982; Wilson 2001; Britton-Simmons 2004). In 2000, a weedy strain of the tropical green alga *Caulerpa taxifolia* (M. Vahl) C. Agardh (Caulerpales) was introduced to southern California and, after a multi-year and multi-million-dollar effort, was declared eradicated in 2005 (Merkel and Associates 2005). Since 1999, the Asian brown algae *Undaria pinnatifida* (Harvey) Suringar (Laminariales) (Silva et al. 2002) and *Sargassum filicinum* Harvey (Fucales) (Miller et al. 2007) and the cosmopolitan red alga *Caulacanthus ustulatus* (Turner) Kützing (Gigartinales) (Zuccarello et al. 2002; Miller 2004) have been introduced to southern and central California and continue to flourish.

In California, many of these introduced seaweeds are found in human-influenced, disturbed bays and harbors on the mainland. *Undaria* was discovered in southern California harbors and Monterey Harbor in 2000–2001 and Baja California, Mexico in 2003 (Silva et al. 2002; Aguilar-Rosas et al. 2004). In 2004, the Invasive Species Survey team (Moss Landing Marine Labs) reported the most recent discovery of *Undaria* in San Diego Harbor. Most of the California populations are limited to harbors and their artificial substrates, especially floats, piers, and boat hulls. However, the population at Santa Catalina Island addressed in this paper is strictly subtidal, persisting at low densities in and around a *Macrocystis pyrifera* community.

Sargassum filicinum, native to the warmer parts of Japan and Korea, has not been reported as an invasive species prior to its arrival in California. In contrast, *Undaria pinnatifida*, native to southeastern Russia, Japan, northern China, and Korea, is an aggressive invasive species in the Mediterranean Sea, England, Atlantic Europe (where it was accidentally introduced and then propagated as a crop), New Zealand, Australia, Argentina, and Baja California, Mexico (Silva et al. 2002; Aguilar-Rosas et al. 2004). A variety of dispersal events (single introductions, multiple introductions, local site-to-site dispersal) as well as various microevolutionary processes (founder's effect, bottlenecks, selection for novel, locally adapted gene combinations) are responsible for *U. pinnatifida*'s worldwide success (Voisin et al. 2005). Uwai et al. (2006) traced the multiple Japanese origins of worldwide populations using molecular methods and speculated that the California (their study included populations from San Pedro, Santa Barbara, and Monterey but not Santa Catalina Island) and Mexican populations were introduced via shipping vectors.

Since 1980, we have conducted 180 multi-day subtidal survey expeditions throughout the eight California Channel Islands with the Tatman Foundation's Channel Islands Research Program (CIRP). During these trips, teams of biologists and volunteers carried out reconnaissance surveys at a broad spectrum of locations to evaluate the distribution and abundance of marine plant and animal species. Our combined experience and network of biologist contacts have provided early documentation of the arrival of *Undaria pinnatifida* and *Sargassum filicinum* at the Channel Islands. Here we report what we have learned from our focused surveys of these non-native seaweeds.

MATERIALS AND METHODS

Following the initial record of *U. pinnatifida* at Button Shell Cove in May 2001, we distributed e-

Table 1. Distribution and number of Channel Islands Research Program reconaissance survey sites from 2001 through 2007.

	Number of sites per year						
Island	2001	2002	2003	2004	2005	2006	2007
San Clemente	17	8	10	9	4	0	10
Santa Catalina	19	12	12	15	11	22	14
Santa Barbara	0	6	0	0	7	3	0
San Nicolas	0	6	0	0	0	0	0
Anacapa	4	3	2	5	7	5	8
Santa Cruz	2	1	13	15	7	11	10
Santa Rosa	0	5	5	5	5	3	0
San Miguel	0	6	0	8	6	0	0

mail messages and posters to alert southern California scientific and recreational divers about this new island invader, requesting notice if this species is encountered. From 2001–2007, our reconnaissance surveys covered representative sites around the eight Channel Islands (Table 1), including sheltered coves where we predicted that *U. pinnatifida* might establish. We also carried out a series of population surveys at Button Shell Cove, initially in June and September 2001, then annually in April and May from 2002 through 2007, with occasional other visits. Surveys consisted of three diver-pairs searching throughout this small cove, in both rocky and soft-bottom habitats, at depths ranging from 2 to 25 m. All *U. pinnatifida* encountered was collected to the extent feasible. Collected plants were categorized as recruit (<20 cm blade without lobes and midrib in evidence only near base), juvenile (blade with full midrib, but no evidence of sporophyll), immature (blade with developing sporophyll) or mature (blade with fully formed sporophyll).

After our discovery of the initial specimen of *S. filicinum* at Santa Catalina Island in April 2006, we once again spread the word to divers to watch for this invasive species and report observations to us. We carried out reconnaissance surveys during 2006–2007 at representative locations at Santa Catalina and five other islands (Table 1). Wherever *S. filicinum* was found, we estimated abundances and recorded distribution patterns and life history information.

RESULTS

Undaria pinnatifida

Initial discovery. On May 10, 2001, Steve Madaras, a dive boat operator and his friend Koji Ozaki, an underwater photographer from Japan, were diving for halibut at Button Shell Cove, a cove east of Long Point, Santa Catalina Island (Fig. 1).

Mr. Ozaki recognized kelp growing at 20 m as *Undaria pinnatifida* (Harvey) Suringar, or wakame. Mr. Madaras contacted the first author and provided a specimen on May 23, 2001.

Subsequent surveys. On June 10–11, 2001, six divers descended at the Button Shell Cove site to 20 m and immediately found the reported population. We also explored shallow water in the vicinity and adjacent sites near White's Landing and Hen Rock.

The majority of the population at Button Shell Cove grew on *Chaetopterus* worm tubes in soft sediment, at depths between 19 and 26 m. Other seaweeds present on worm tubes were *Pelagophycus porra* (Leman) Setchell, *Agarum fimbriatum* Harvey, *Laminaria farlowii* Setchell, *Dictyopteris undulata* Holmes and juvenile *Eisenia arborea* Areschoug. We collected 121 individuals from this depth. Most plants bore sporophylls, and many blades were truncated due to apical erosion. We also collected 11 small individuals of *U. pinnatifida* (< 60 cm blade length) in depths of less than 6 m under the pier. Despite a diversity of substrates available under the pier, they grew only on tires. Eight out of the 11 bore sporophylls.

In September 2001, plants were collected at depths between 22 and 24 m (Table 2). Most blades were deteriorated, leaving midribs,sporophylls (some flabby and "spawned out"; others dark and healthy), and holdfasts. No juvenile sporophytes were observed. In April and May 2002, we collected *U. pinnatifida* on rocky substrates in the

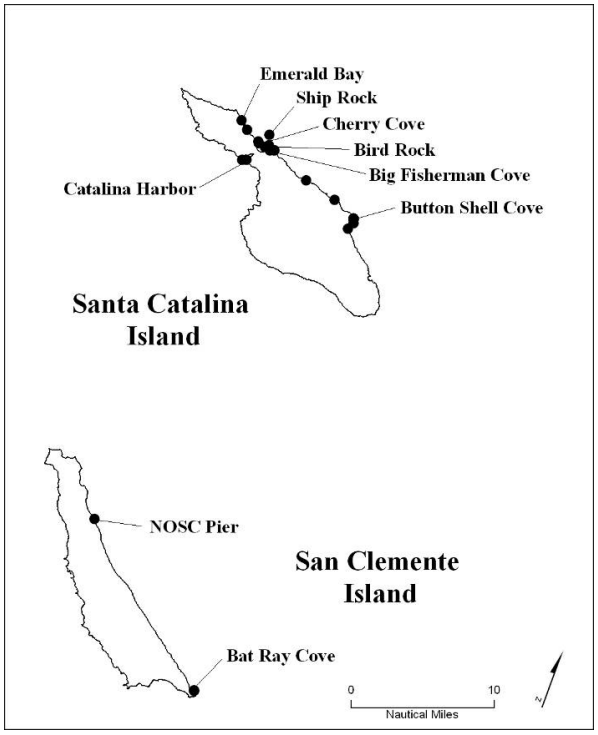

Figure 1. Map showing selected survey sites at Santa Catalina and San Clemente islands to the south and Italian Gardens to the north of Long Point. *Undaria pinnatifida* was absent at these sites, at all depths.

Table 2. *Undaria pinnatifida* population surveys at Santa Catalina Island.

Site	Date	Substrate	*Undaria* depth (m)	# Divers	# *Undaria*	Notes
Button Shell	5/10/2001	Worm tubes on sand	20	2	No data	Initial discovery by Steve Madaras & Koji Ozaki. Voucher collected.
	6/10–11/2001	Worm tubes on sand	19–26	6	121	First survey of rock & sand habitats throughout cove.
		Car tires under pier	6	6	11	Young *Undaria*.
	9/6/2001	Worm tubes on sand	22–24	24	33	CA Dept. Fish & Game divers aided surveys.
	9/25/2001	Worm tubes on sand	24	7	54	This single patch of *Undaria* apparently was missed on prior survey.
	4/19/2002	Worm tubes & snail shells on sand; metal & plastic debris; cobble/rock w/kelp plastic debris; cobble/rock w/ kelp	6–26	6	559	*Undaria* not counted by habitat. Most on worm tubes at 15–26 m. Few on cobble/rock at 10–15 m. Juveniles predominated.
	5/10/2002	Cobble/rock w/ kelp	6–20	10	482	
	5/13/2003	Worm tubes & snail shells on sand; metal debris; pier pilings; cobble-rock w/kelp debris; pier pilings; cobble/rock w/ kelp	6–25	6	638	*Undaria* not counted by habitat. Most on worm tubes at 15–22 m. or on cobble/rock at 10–15 m. Juveniles predominated.
	5/14/2004	Cobble/rock w/kelp	5–15	6	63	*Undaria* mostly on main kelp reef.
		Worm tubes & snail shells on sand	8–23	6	16	*Undaria* in shallow eelgrass bed.
		Car tires under pier	6	6	3	Young *Undaria*.
	5/1/2005	Cobble/rock w/ kelp	3–12	5	234	Few mature adult *Undaria*.
	4/23/2006	Cobble/rock w/ kelp	5–14	6	90	Earlier in April, USC class collected undetermined # of *Undaria*.
	5/14/2007	Cobble/rock w/ kelp	6–16	6	203	96% of *Undaria* found at 6–13 m depths on kelp reef.
White's Landing	5/14/2004	Metal debris on sand	12	6	83	Single patch of *Undaria* was directly offshore from pier.

Macrocystis pyrifera (C. Agardh) Linnaeus forest at Button Shell Cove at 6–12 m depth, and observed that it was less common at greater depths. In subsequent years, *U. pinnatifida* has not been found in the deep kelp community (Table 3). Undaria recruits in late winter (February-March) with the native kelps, is reproductive in spring and summer, when it begins to deteriorate, and disappears by late October. From 2001 through 2007, we tracked recruits, juveniles, and immature and mature plants (Tables 2, 3; Fig. 2). The population size and timing of development fluctuates. For example, the phenological pattern in 2002, 2003, and 2005 was similar, with 10–20% mature individuals in May, but 90% of the individuals were mature in June 2001 and May 2007. These results also indicate that the population as a whole is stable year to year, despite

Table 3. Sites at Santa Catalina (SCA) and San Clemente (SCL) islands where Undaria and S. filicinum were observed. Abundances: absent (-); 1–10 plants (+); 11–100 plants (++); 101–1000 plants (+++); >1000 plants (++++); not determined (X).

Island	Site	Latitude	Longitude	Date	*Undaria*	*S. filicinum*
SCA	Button Shell Cove	33° 24.3N	118° 22.0W	6/10/01	+++	-
	"	"	"	9/6/01	++	-
	"	"	"	9/25/01	++	-
	"	"	"	4/19/02	+++	-
	"	"	"	10/21/02	-	-
	"	"	"	5/13/03	+++	-
	"	"	"	5/14/04	+++	-
	White's Landing	33° 23.5N	118° 22.1W	5/14/04	++	-
	Button Shell Cove	33° 24.3N	118° 22.0W	2/10/05	++	-
				4/30/05	+++	-
	WMSC Intake Pipes	33° 26.8N	118° 29.1W	4/20/06	-	++
	West Cherry Cove	33° 27.1N	118° 30.1W	4/21/06	-	+
	Button Shell Cove	33° 24.3N	118° 22.0W	4/23/06	+++	-
	West Emerald Bay	33° 28.1N	118° 31.7W	4/24/06	-	+
	Hen Rock	33° 24.0N	118° 21.9W	9/12/06	-	++
	Button Shell Cove	33° 24.3N	118° 22.0W	9/12/06	-	-
	Pumpernickel Cove	33° 26.9N	118° 28.8W	11/1/06	-	+++
	WMSC Intake Pipes	33° 26.8N	118° 29.1W	11/1/06	-	+++
	Isthmus Reef	33° 26.9N	118° 29.5W	11/2/06	-	++
	Bird Rock	33° 27.1N	118° 29.3W	11/2/06	-	+++
	Big Geiger Cove	33° 27.6N	118° 31.1W	11/4/06	-	+++
	Empire Landing*	33° 26.4N	118° 27.8W	11/4/06	-	X
	Twin Rocks*	33° 25.1N	118° 23.4W	11/4/06	-	X
	E of East End Quarry*	33° 19.3N	118° 18.2W	11/25/06	-	X
	Casino Point*	33° 20.9N	118° 19.5W	12/9/06	-	X
	Button Shell Cove	33° 24.3N	118° 22.0W	5/14/07	+++	-
	Hen Rock	33° 24.0N	118° 21.9W	5/14/07	-	+
	Goat Harbor	33° 25.1N	118° 23.7W	5/14/07	-	+++
	Ripper's Cove	33° 25.7N	118° 26.0W	5/14/07	-	+++
	Button Shell Cove	33° 24.3N	118° 22.0W	7/10/07	++	-
	East Cherry Cove	33° 27.0N	118° 30.0W	7/12/07	-	+++
	Bird Rock	33° 27.1N	118° 29.3W	10/25/07	-	++++
	Pumpernickel Cove	33° 26.9N	118° 28.8W	10/25/07	-	++++
	Pin Rock, Catalina Hbr	33° 25.6N	118° 30.4W	10/26/07	-	+++
	West Catalina Hbr	33° 25.5N	118° 30.7W	10/26/07	-	++++
	Button Shell Cove	33° 24.3N	118° 22.0'W	10/27/07	+	+++
	Ship Rock	33° 27.8N	118° 29.5W	10/28/07	-	+++
SCL	South of NOSC Pier	32° 58.4N	118° 31.8W	5/12/07	-	+
	Bat Ray Cove	32° 49.2N	118° 21.05W	5/13/07	-	+++

*Record from W. Bushing, Avalon, CA

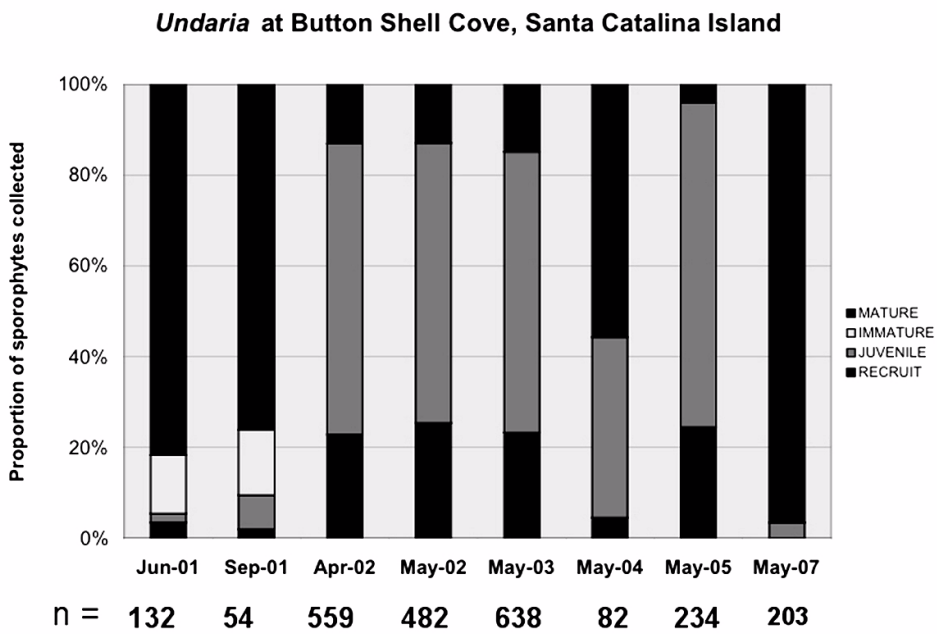

Figure 2. Age distribution of *Undaria pinnatifida* sporophytes at Button Shell Cove, Santa Catalina Island, 2001–2007. Bars represent proportion of collections in each age class (recruit, juvenile, immature, mature; see Materials and Methods for criteria). Total number collected each year (n) is presented below the graph.

removal of plants that we encounter in our surveys each year.

Annually, we searched for *U. pinnatifida* at Santa Catalina Island and throughout the Channel Islands during a series of CIRP cruises (Tables 1, 2, 3). Although we alerted scientists and divers, we have received no reports of *U. pinnatifida*, nor have we discovered any other populations in the course of our surveys at the eight Channel Islands.

Sargassum filicinum

Initial discovery. On April 8, 2006, we discovered a population of *Sargassum filicinum* at the Intake Pipes, a rocky point north of Big Fisherman Cove near the Wrigley Marine Science Center and the town of Two Harbors, on Santa Catalina Island, CA (Miller et al. 2007, Fig. 1). Discovery of the initial specimen of *S. filicinum* by the first author occurred less than two weeks prior to a CIRP survey trip to the island that included Japanese phycologist Dr. Hiroshi Kawai, who confirmed the species identity and collected specimens for molecular analysis, allowing us to pinpoint its likely origin as the Seto Inland Sea, Japan (Miller et al. 2007). In April 2006, there were more than 30 plants (0.3–1.5 m tall) at depths between 4 and 12 m at the Intake Pipes site. Some individuals were young, with rosettes of fern-like, spiny leaves, but most were mature, bearing elongate receptacles and the characteristic spherical-elliptical vesicles of *S. filicinum*. We also observed plants in sheltered habitats at Cherry Cove (2 plants at 4 m and 13 m depths) and Emerald Bay (4 plants at 7 m depth), both nearby sites on the leeward west end of the island (1.8 km and 3.0 km NW of Intake Pipes; Fig. 1). These three populations at Santa Catalina Island may have been the result of a single introduction and subsequent local dispersal.

In the year following its discovery on the west end of Santa Catalina Island, *S. filicinum* spread rapidly along the leeward (north) side of Santa Catalina to the east end (Table 3). In 2007, *S. filicinum* was confirmed at more sites along the leeward (north) side of Santa Catalina Island. In May, juvenile plants densely carpeted shallow horizontal rock surfaces at these sites (Fig. 3). In October 2007, we documented populations at Button Shell Cove and Ship Rock (Fig. 1) that were absent during surveys in May and July 2007. Within

Figure 3. Juvenile *Sargassum filicinum* covering available substrate at 6 m depth, Goat Harbor, Santa Catalina Island. Photo by Dan Richards.

one year, *S. filicinum* spread at Bird Rock (Fig. 1) from a single patch at the east end to scattered dense patches along the entire west side. In April 2007, drift specimens of *S. filicinum* were observed at Catalina Harbor, on the windward (south) side of Santa Catalina Island (Fig. 1). Dives in October 2007 at both sides of the outer mouth of the harbor confirmed the presence of patchy populations of *S. filicinum*. The pattern of large plants surrounded by juveniles suggests an early stage of invasion at these sites. During these 12 dives in October, with 2 observers spending a total of 8 hours underwater at 6 sites, we counted approximately 5000 plants.

Figure 4. Mature *Sargassum filicinum* at 6 m depth, Bat Ray Cove, San Clemente Island. Photo by Dan Richards.

In May 2007, we surveyed 10 sites along the leeward coast of San Clemente Island, from Northwest Harbor to Pyramid Cove. We found a single plant south of the NOSC Pier, about mid-island (Table 3, Fig. 1). At Bat Ray Cove just north of Pyramid Head (Fig. 1), we found a 10 m by 20 m patch of reproductive, senescent *S. filicinum* at 6–13 m depth in an open, sandy habitat (Table 3, Fig. 4). During May-September 2007, we surveyed 8 sites at Anacapa Island and 10 sites at Santa Cruz Island; *S. filicinum* was absent (Table 1).

DISCUSSION AND CONCLUSIONS

The pattern of spread of these two species at the Channel Islands is unexpected. *Undaria pinnatifida* was reported at harbors throughout the southern California Bight, and at Santa Catalina Island and Monterey Harbor, within a year of its discovery in Los Angeles Harbor (Silva et al. 2002). Since its initial introduction to Monterey, *U. pinnatifida* has not spread in central and northern California, despite predictions that it would do so (Silva et al. 2002; Thornber et al. 2004). On the other hand, *S. filicinum* was discovered in Long Beach Harbor in 2003 but was not reported again until 2006 (Aguilar-Rosas et al. 2007; Miller et al. 2007). It then spread explosively on Santa Catalina Island and has been observed at San Clemente Island, a popular fishing destination, where we predict it too will spread rapidly. The subtidal habitats at Anacapa Island and the southeast portion of Santa Cruz Island are similar to those in the southern islands and probably suitable for the establishment of S. filicinum. However, despite extensive boat traffic, a potential vector for establishment, we have yet to observe it at those locations.

It is interesting that both *U. pinnatifida* and *S. filicinum* established at Todos Santos Island in Baja California, Mexico as well as Santa Catalina Island in California. Neither of these sites are major harbors with international shipping. We hypothesize that *S. filicinum* arrived in California via international shipping, but has spread to Santa Catalina and San Clemente islands via pleasure boats (both are frequented by boats berthed in Los Angeles and San Diego area harbors). This may be the case for *U. pinnatifida* as well.

Undaria pinnatifida has demonstrated a broad ecological tolerance, having established itself globally. It is a fast-growing, extremely fecund opportunist that is precociously fertile, with a microscopic, cryptic gametophytic stage in its life history (Saito 1975; Thornber et al. 2004). These traits make it difficult to eradicate once it has established. Still, its growth and longevity are controlled by temperature (Oh and Koh 1996), which may limit its spread in southern California.

The depths at which *Undaria* initially established itself at Button Shell Cove far exceed 15 m reported as a maximum depth for other populations, both native and introduced (Saito 1975; Silva et al. 2002; Russell et al. 2008) and may reflect a refuge from warmer surface waters. *Undaria pinnatifida* is also sensitive to wave exposure, which may limit it to harbors and sheltered coves (like Button Shell Cove), although it exhibits a very different pattern in New Zealand, where it is spreading aggressively to the open coast (Russell et al. 2008). We would predict that *U. pinnatifida* would establish at sheltered coves at Anacapa and Santa Cruz islands, with pleasure boats from *U. pinnatifida*-infested berths in Long Beach, Los Angeles, Santa Barbara, Ventura, and Channel Islands harbors as its vectors. But this has not been the case.

Populations of *U. pinnatifida* at Santa Catalina Island are strictly annual, with a pattern of development similar to that in its native habitat (Fig. 2; Saito 1975). *Undaria pinnatifida* and *S. filicinum* share similar phenologies, recruiting in late winter, growing quickly, becoming reproductive early, and dying in late summer or fall. The Santa Catalina Island population of *U. pinnatifida* does not exhibit a burst of recruitment in the fall (Thornber et al. 2004) and overlapping generations as in New Zealand (Hay and Villouta 1993), and we have not observed extensive herbivory by kelp crabs, as reported in Santa Barbara Harbor (Thornber et al. 2004).

Sargassum filicinum, like *S. muticum*, is well adapted for widespread dispersal to and rapid colonization of new areas (Nyberg and Wallentinus 2005). Like *S. muticum*, this species is monoecious, bearing both male and female conceptacles; individuals are thus capable of self-fertilization. It is extremely fecund, with large and abundant reproductive receptacles. Fertile fragments are buoyant due to air-filled vesicles and can readily disperse locally. Its establishment, like that of *S. muticum* and *U. pinnatifida*, may be promoted by its precocious fertility, which is presumably related to its essentially annual growth pattern (Miller et al. 2007). Again like *S. muticum*, it is a fast-growing opportunist, producing copious recruits in overlapping generations and colonizing a variety of habitats. Unlike *S. muticum*, it occupies a relatively narrow depth range (6–19 m) and apparently has a narrower temperature tolerance, since so far it has invaded only the warmest habitats in California. We speculate that *S. filicinum* is adept at local dispersal but that long range dispersal is episodic. This would account for its slow progress on the mainland coast, which is interrupted by stretches of sand and man-made structures, unlike the uninterrupted habitat available around Santa Catalina Island.

Although we did not find *U. pinnatifida* dispersing to new sites and observed that *S. filicinum* is spreading rapidly at Santa Catalina Island and has reached San Clemente Island, we also predict that the situation could change. It may require repeated introductions of *U. pinnatifida* under a narrow set of conditions to initiate the establishment of a population in the subtidal habitats around the Channel Islands. We speculate that changes in the cover and density of *Macrocystis*, due to changes in ocean climate, e.g., ENSO events and climate change (Stachowicz et al. 2002) and biotic interactions, e.g., domination by herbivores like urchins, could create conditions conducive to introduction (Valentine and Johnson 2003, 2004)—or not (Valentine and Johnson 2005). The current boom of *S. filicinum* could continue, or equilibrate with populations of native species, much as *S. muticum* has at Santa Catalina Island relative to its explosive growth (Ambrose and Nelson 1982) after an ENSO event. It remains to be seen how *U. pinnatifida* and *S. filicinum* populations will interact with those of native species (seaweeds and herbivores) and the non-native *S. muticum* over time. We hope that our observations stimulate detailed ecological studies of these new members of the community.

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INCREASED UNDERWATER NOISE LEVELS IN THE SANTA BARBARA CHANNEL FROM COMMERCIAL SHIP TRAFFIC AND THE POTENTIAL IMPACT ON BLUE WHALES (*BALAENOPTERA MUSCULUS*)

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Abstract—The Channel Islands National Marine Sanctuary (CINMS) and the surrounding waters are considered an urban coastal environment, yet home to a diversity of marine organisms. Understanding the interactions between human activity and the marine ecosystem is vital to its sustainability. In our study, we investigated the acoustic environment in the region, focusing primarily on the addition of anthropogenic sound produced by commercial ship traffic. Our study used a passive, broadband, high-frequency acoustic recording package (HARP) to record ambient noise levels and the contribution of noise from commercial ship traffic to the acoustic environment. Recorded ship sound levels were identified using ship-passage records known as Automatic Identification System (AIS). Our analyses of ambient noise levels from July to October 2007 showed elevated levels of 15–25 dB in the 10–150 Hz frequency band when ships were nearby (<4 km). There were on average 18 ships passing through the channel every day, resulting in approximately three hours per day of elevated noise levels from commercial ship traffic. The shipping activity in the Santa Barbara channel was highest at noon and midnight. Increased background noise levels from the ships have the potential to impact the endangered blue whales utilizing the Santa Barbara Channel. When ships were nearby, blue whale calls were not detected. Although it is unclear whether the whales ceased calling when a ship was present, or the calls were masked by the increased noise, both situations have the potential to impact the whales' ability to carry out normal behaviors in the Santa Barbara Channel. The results of this research will advance scientific understanding of human noise in the marine environment, inform policy decisions for noise in the Sanctuary, and serve as a model for addressing noise pollution in other marine sanctuaries.

INTRODUCTION

The pervasive nature of noise pollution from commercial ships threatens the health of many coastal regions, including the Channel Islands National Marine Sanctuary (CINMS or Sanctuary). Given the Sanctuary's ecologically important and sensitive habitats and populations of marine mammals, large vessel traffic is an ongoing management concern. The shipping lanes of the Santa Barbara Channel (SBC) overlap the eastern portion of the CINMS, with at least 6500 vessels (43% of all U.S. shipping trade) passing through the Sanctuary annually (CINMS January 2009). Our research focuses on the potential acoustic effects of commercial ship traffic, which range from interference with communication in marine mammals and fishes to degradation of habitat quality and/or prevention of recovery in protected systems. It is important to characterize local shipping traffic in the SBC and determine the level of noise added to the marine environment by commercial ships, in order to assess the level of threat to marine organisms.

As the global commercial shipping fleet increases its size and speed, noise added to the marine environment has intensified; background levels are now elevated at some sites by at least 10 times what they were in the 1960s and have doubled in intensity every decade for the past 40 years (Andrew et al. 2002; McDonald et al. 2006). In the Pacific basin where low frequency sounds can propagate for hundreds of kilometers, this trend is attributed to noise from local and distant ships. However, because of the complex bathymetry in coastal regions like the Southern California Bight, most noise from distant ships will not propagate into the shallow regions. Thus, local shipping traffic is

the dominant source of ship noise in the SBC (McDonald et al. 2008). The objective of this study is to establish noise levels in the SBC, and assess how these levels are influenced by local ship traffic. Results will be discussed in the context of potential impacts on the endangered North Pacific blue whale (*Balaenoptera musculus*).

The SBC includes not only one of the busiest shipping lanes in the world, but is also an important summer foraging region for the endangered North Pacific blue whale population. The whales tend to aggregate in cold, up-welled coastal waters to feed primarily on subsurface concentrations of euphausiids (Croll et al. 1998; Fiedler et al. 1998). Blue whale populations were decimated by commercial whaling from around 300,000 to fewer than 10,000 and are slowly recovering (Barlow 1995). The North Pacific stock estimates are around 2000 and may be one of the largest populations in the world (Barlow 1995; Calambokidis and Barlow 2004). During the feeding months, whales continuously interact with both commercial and recreational vessels in the channel.

Besides the increased risk of direct interaction between ships and whales, the potential acoustic impacts are also heightened. Blue whale calls are predominantly in the low frequencies (15–100 Hz); a frequency range similar to the dominant acoustic energy of ships (Richardson et al. 1995). Most noise generated by large ships is from propeller cavitation, and machinery noise causing vibrations in the hull is a less dominant source. Propeller cavitation results from the formation and collapse of bubbles at the propeller blade tips (Ross 1976). These sounds are radiated into the water column and will propagate to distances dependent on the bathymetry and water column characteristics. Although the sounds lose intensity as the distance from the source increases, the noise from ships has the potential to mask the calls of whales. Blue whales in the North Pacific are known to produce at least four call types (McDonald et al. 1995; Thompson et al. 1996): A and B calls (16 Hz, ~20 s duration), D calls (down sweep from 90–25 Hz, 1–4 s duration), and highly variable amplitude and frequency modulated calls. A and B calls are songs produced by males and possibly function in mate

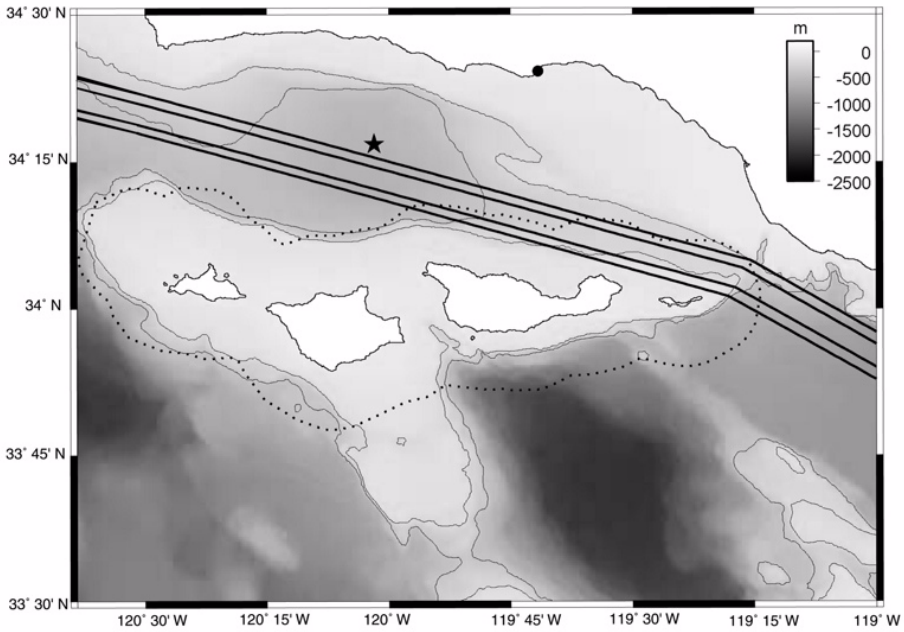

Figure 1. Map of Santa Barbara Channel and the Channel Islands National Marine Sanctuary (CINMS). The dotted line represents the borders of CINMS. The star is the location of the seafloor HARP in the SBC. The contour lines are at 200 and 400 m. The circle is the location of the AIS receiver in Santa Barbara harbor. The solid black lines represent the commercial shipping lanes.

attraction (McDonald et al. 2001). The D calls are recorded from both males and females and are usually associated with feeding behaviors (Oleson et al. 2007a).

The primary goal of this study is to establish background noise levels for the region, in the frequencies utilized by blue whales. Because the region is frequented by ship traffic, the change in noise levels by commercial ships can be characterized. Ultimately, this information can be used to assess the potential threats to the whales.

METHODS

Data Collection

To monitor the acoustic environment within the SBC shipping lanes, a high-frequency acoustic recording package (HARP) was placed in the SBC at 34.32W 120.03N in 530 meters of water (Fig. 1). HARPs are autonomous seafloor-mounted instruments used to provide long-term acoustic recordings, and contain a battery power supply, data acquisition system, hydrophone sensor, acoustic release system, ballast weights, and flotation (Wiggins and Hildebrand 2007). The hydrophone is tethered to the instrument package and buoyed 10 m off the seafloor. The hydrophone employs a two transducer design to provide a high-sensitivity broadband (10 Hz–100 kHz) response, which allows the data acquisition system to record a wide range of sounds, from low frequency ships and baleen whales to high frequency toothed whales and dolphins. HARPs currently store 1920 GB of acoustic data, allowing continuous recording at 200 kHz sample rate (or 200,000 samples per second) for 55 days. The instrument was deployed by the R/V Shearwater on July 13, 2007 and began recording the same day. The instrument stopped recording on October 30, 2007 and was subsequently recovered from the seafloor.

Commercial vessel activity in the SBC was monitored through the Automatic Identification System (AIS) (http://www.navcen.uscg.gov/enav/ais/). AIS is required by all ships over 300 tons to transmit the vessel's characteristics as well as location, speed, and heading information via a VHF signal. An AIS receiving station was set up in Santa Barbara Harbor to continuously archive all ship AIS transmissions in the SBC (Fig. 1). The VHF signal was received with a 124WB Boomer 4 element broadband 2 meter Yagi antenna (Cushcraft Corporation). The strength of VHF signal transmission is dependant on line of sight and atmosphere conditions; therefore some AIS transmissions were not received. The AIS signal was fed through a radio(Icom IC-PCR1500 receiver, 1 channel) into a computer. Using the program ShipPlotter (http://www.coaa.co.uk/shipplotter.htm), the signal was decoded, played in real time, and archived for later analysis. The archived data from July 13, 2007 to October 30, 2007 were downloaded and analyzed using specific functions developed in MATLAB (version 2007b, The MathWorks, Natick, MA). For this analysis, only ships in the shipping lanes were analyzed. Although other vessels utilize the region and contribute noise to the environment, they are not required to have AIS, making it difficult to quantify the contribution of noise from these smaller vessels.

Data Analysis

The broadband acoustic data from the HARP were processed to determine average ambient noise levels, both with and without ships nearby, to characterize ship traffic, and to detect blue whale calls. All data were calibrated based on the frequency response curve of the hydrophone from calibration measurements performed in our laboratory and at the U.S. Navy's Transducer Evaluation Center (TRANSDEC) facility in San Diego. The AIS data were processed to identify times ships were nearby the HARP, and to characterize ship traffic.

To determine the background noise levels in the SBC from July through October 2007, times when ships were distant (at least 9 km distance from the instrument) were manually selected from the data. Noise levels are expressed as the distribution of mean square pressure per unit frequency. To calculate these levels, a fast-Fourier transform was performed on 20 seconds of time (400,000 samples). The fast-Fourier transform results in mean pressure squared values for 0–10,000 Hz. The data are then converted to sound pressure levels expressed as decibels referenced to a unit pressure density. A total of 366 different 20-second samples were analyzed at random from July through October 2007. To get the average noise level, each frequency bin was averaged together for all selected 20-second samples.

Average noise levels when a ship was near the HARP (less than 4 km) were determined by combining the AIS data with the acoustic recordings. From the AIS, the time of the closest point to the HARP for a given ship was determined. The time that corresponded to an individual ship was then manually selected in the acoustic data. A total of 80 ships were analyzed using the same protocol as described above to determine the average noise level when ships are nearby.

Both the AIS and acoustic data were used to characterize ship traffic in the SBC. The mean number of ships, standard deviations, and standard errors are reported from both the AIS and acoustic data. The mean ship speed, standard deviation, and standard errors from the AIS data are reported. The AIS data includes geographical information; therefore analyses of the number and speed of ships were performed on ships in the entire channel and ships in just the shipping lanes. AIS data contains information on ship type, so percentages of ship types in the channel are disclosed.

The number of ships that passed the instrument was determined by an analyst scanning the acoustic data for periods when a distinct acoustic signature from a ship was present. This served as a comparison to the mean number of ships per day detected by AIS. In addition, the time of acoustic detections of ships was analyzed to investigate daily shipping patterns. For this analysis, the data set was expanded to include ships from November 2006 to October 2007.

The contribution of ship noise to the environment was calculated based on the difference in average sound pressure levels in each frequency (10–1000 Hz) when local ships were nearby (<4 km) to when ship traffic is low. This difference served as a metric to quantify the increase in noise levels as a result of ship traffic. To estimate the average number of hours per day that sound levels were increased from ships, the average duration (d) of increased noise levels as the ship passed the instrument was multiplied by the number of ships per day (n) to arrive at the percent of the day ambient noise levels are elevated: $n * (d / 60)$ = hours. The duration that sound pressure levels are elevated depends mainly on the size and speed of the ship; the duration that levels were elevated by at least 15 dB averaged 10 minutes for all ships analyzed.

The acoustic data were also scanned for the presence of blue whale calls. The calls of many baleen whale species are stereotyped and well known. Detection and classification of stereotyped mysticete calls are carried out using automatic detectors (Oleson et al. 2007b). The acoustic data from September 2007 and archived data from the same location in September 2005 were analyzed for the presence of blue whale B calls using the spectrogram correlation function within the software program Ishmael (Mellinger 2002). From previous studies with blue whale B calls (Oleson et al. 2007b), this has proved to be an effective detection method.

RESULTS

A four month average of acoustic energy in the SBC when local ships were not nearby (>9 km) shows that the sound levels in the low frequency band (10–1000 Hz) ranged from 56 to 90 dB re: $1Pa^2/Hz$ (Fig. 2). During this period the blue whales calls are a dominant source of acoustic energy, and are elevated above the background by 10 dB re: $1Pa^2/Hz$ at 16 Hz (the fundamental frequency of the blue whale B song call). The subsequent peaks are harmonics of the fundamental frequency (32 Hz and 48 Hz). The number of automatic detections of B calls per day ranged from 609 to 919.

When local ships are nearby (<4 km), sound pressure levels in the lower frequencies (0–150 Hz) increase by 15–25 dB when compared to normal background levels. The fundamental frequency of the blue whale call (16 Hz) is no longer detected above the background levels when a ship is within 4 km of the recording instrument (Fig. 2). However the third harmonic of the blue whale call is slightly above the background (Fig. 2), suggesting that the whales are calling when a ship is present, but the fundamental frequency of the call is masked.

Based on detections of ships in the acoustic data, there are ~19 ships per day passing the acoustic instrument, compared to ~15 ships detected by the AIS (Table 1). The majority of ships detected by the AIS were cargo ships transiting the channel (Table 2). The average speed from the AIS over this four-month period was ~15 knots in the entire channel; however the average speed for ships in the lanes was higher (~20 knots) (Table 1).

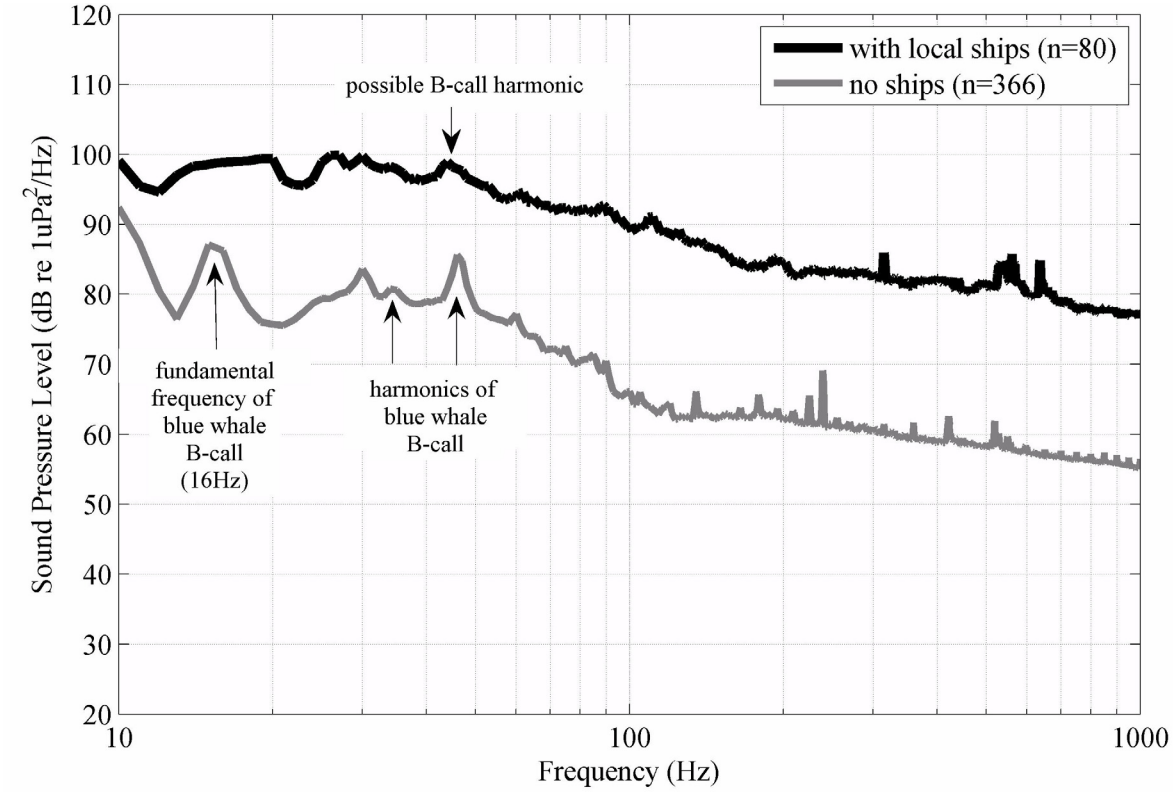

Figure 2. Comparison of sound pressure levels in the Santa Barbara Channel when ships are nearby (<4 km) and ships are distant (>9 km). The data are from July 2007 to October 2007.

Based on the number of ships and the duration of the elevated noise levels, the ambient noise levels are elevated by 15–25 dB for an estimated 3.1 hours per day. The increased levels of noise do not appear to be evenly distributed throughout the day; distinctive peaks in shipping activity exist at noon and midnight (Fig. 3).

DISCUSSION

The level of ambient noise in the SBC is elevated by 15–25 dB when a commercial vessel traveling in the northbound lane is <4 km from our acoustic recorder. The duration of the increased background noise is approximately 3.1 hours per day. This pattern is likely true for a 4 km distance outside the shipping lanes as a ship is transiting the channel. As distance to the shipping lanes decreases the levels will increase; likewise as one moves greater than 4 km from the lanes, the increase in sound levels will diminish as a function of that distance.

When ships were < 4 km, the fundamental frequency of blue whale B calls was no longer detected above ambient noise levels. This result might indicate that blue whales are either not present or do not call when ships are nearby. However, results of blue whale detections from the acoustic data show that calling animals were present during this time, and aerial surveys corroborate this finding (http://channelislands.noaa.gov/). Furthermore, the harmonic at 48 Hz was slightly elevated above the background, suggesting that whales are calling but their calls are masked by the increased noise from commercial ships (Fig. 2).

Peaks in shipping activity occur at noon and midnight, and are most likely related to patterns of activity at the ports of Los Angeles and Long Beach. Blue whale B calls are primarily made during crepuscular hours (Oleson et al. 2007b; Wiggins et al. 2005), when ship traffic in SBC appears to be the least intense, so it is possible that noise from commercial ships will have minimal impacts on the mating calls of blue whales. Blue whale D calls

Table 1. Comparison of ship traffic: July 13 to October 31, 2007.

	Data	Location	Mean	Standard deviation	Standard error
# Ships	AIS	Channel	15.6	4.5	0.46
# Ships	AIS	Shipping lanes	11.7	4.3	0.44
# Ships	Acoustics	HARP	18.8	10.8	1.9
Speed (knots)	AIS	Channel	15.2	2.6	0.26
Speed (knots)	AIS	Shipping lanes	19.7	2.2	0.23

associated with feeding peak at dawn and dusk, but also are detected throughout the day (Oleson et al. 2007b). Therefore, if the noise from shipping traffic masks blue whale D calls in a manner similar to B calls, the increased ship activity at midday might interfere with some blue whale feeding behavior.

The biological significance of the elevated ambient sound pressure levels is not clear; comparisons of background noise measurements in other regions, with different levels of ship traffic, put the results for SBC in perspective, in terms of the levels of exposure to the animals utilizing the region. Sound pressure levels from North Pacific offshore deep sites (off Point Sur and San Nicolas Island) are similar to SBC without ships nearby (Andrew et al. 2002; McDonald et al. 2006). However, when ships are nearby the sound pressure levels in the SBC are ~5–10 dB greater than those of the North Pacific sites (Fig. 4). When local ships are present in the SBC, the levels are 0–5 dB greater than the average levels in the highly industrialized Gulf of Oman (Wagstaff and Aitkenhead 2005). The Scotian Shelf measurement, made in the 1960s (Piggott 1964), is from an area of low local ship traffic, and as expected the sound levels are below those in the SBC; without nearby ships by 0–15 dB (10–200 Hz) and 15–35 dB below SBC when a ship is nearby (Fig. 4). This suggests that even when local ships are not present in the SBC, the levels are higher than measurements in the 1960s. The west side of San Clemente Island has little local ship traffic and is shadowed from the propagation of distant shipping by the adjacent deep canyons and shallow banks (McDonald et al. 2008). This site is over 40 dB less than SBC when local ships are present. Because the decibel scale is a logarithmic scale, 40 dB equate to a ten-thousand (10^4) increase in acoustic power. Although we do not have measurements of the pre-human ocean noise levels, when the animals evolved, the site off San Clemente offers a potential baseline to compare ambient noise levels that animals are exposed to today.

The level of noise generated by ships is related to the size, speed, and power of a ship along with a number of other factors, including type, propeller, engine, age, and any damage. In general, larger, faster ships generate more noise because they produce more propulsion power which is converted into acoustic power (noise) via bubble cavitation (Ross 2005). Reducing ship speed has been a possible management strategy to reduce noise levels and ship strikes (Laist et al. 2001). Although this will result in decreased noise levels, the degree of the reduction is frequency dependent. Arveson and Vendittis (2000) compared sound levels from the

Table 2. Types of ships in Santa Barbara Channel (July 13 to October 31, 2007).

Ship type*	Total number	Percentage
Anti-pollution	3	0.56%
Cargo ship	404	75.94%
High speed craft	1	0.19%
Other ship	23	4.32%
Passenger	7	1.32%
Tanker	52	9.77%
Tug	7	1.32%
Dreg vessel	2	0.38%
Fishing vessel	1	0.19%
Military vessel	1	0.19%
Pleasure vessel	8	1.50%
Research vessel	23	4.32%

*Ship types defined based on AIS data designation.

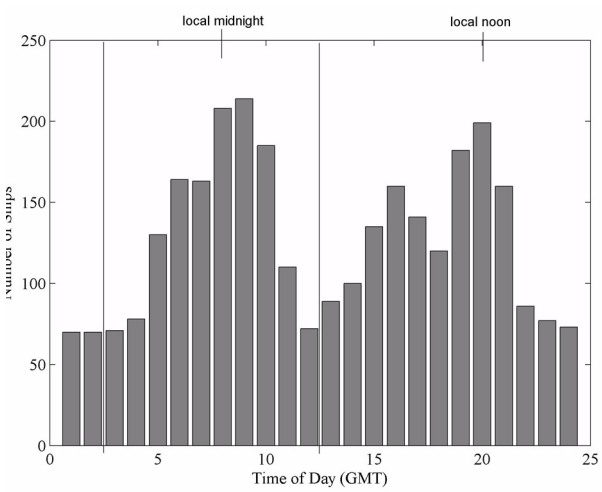

Figure 3. Acoustic daily ship activity patterns. The time a ship was closest to the HARP was used for this analysis. The y-axis describes the total number of ships observed at the subsequent time of day. Data set was expanded to include ships from November 2006 to October 2007.

same ship as it changed speed. By controlling for ship speed they found that at low frequencies (<150 Hz, the frequencies of blue whale calls), there was a 21 dB decrease as the ship slowed from 14 knots to 8 knots; however, at 10,000 Hz (the frequency of dolphin whistles), there is only a 10 dB decrease in noise for the same speed reduction. Therefore, management strategies should determine the frequencies that they are interested in reducing before advocating for speed reduction of ships to lower noise levels.

Another complication with speed reduction in terms of decreasing noise output is the impact on the biology. An animal's perception of a sound plays an important role in determining temporal threshold shifts and/or permanent hearing loss. This is especially important for more resident species that are not capable of leaving an area during increased noise levels. For some fishes it is known that they have significant increased levels in stress hormones when ship noise is present (Wysocki et al. 2006); however more experimental data is needed to determine the impact of a longer quieter sound,

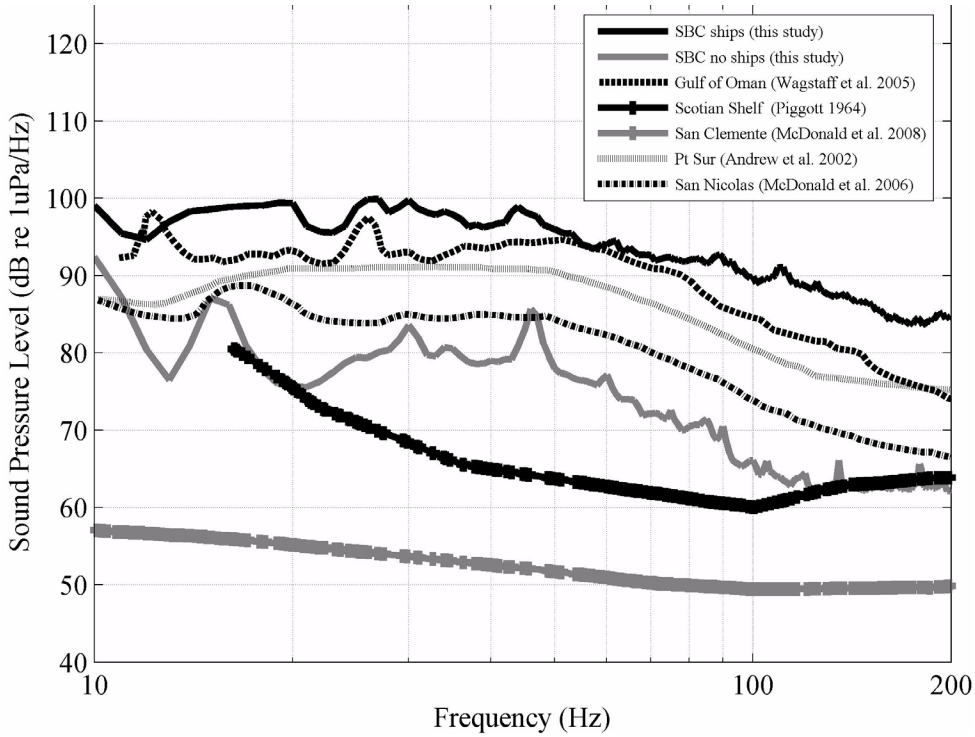

Figure 4. Comparison of low frequency sound pressure levels in the Santa Barbara Channel to other coastal and deep ocean regions.

compared to louder shorter sound (e.g., the result of slowing a ship).

The noise levels in SBC are high compared to other coastal regions, and the potential for impacts on the marine mammals and fishes seems inevitable. Future modeling of sound propagation in the channel will help elucidate characteristics of the basin that might contribute to the high noise levels. A future component to this study will be to compare the SBC to other regions in the Sanctuary to identify quieter regions, either from sound propagation and/or proximity to shipping lanes. If elevated noise levels are influencing the health of the region, the comparison between sites will offer a measure of this impact. Furthermore, determining behavioral and auditory impact on blue whales through the deployment of acoustic tags when a ship is present will also help evaluate the impact of elevated noise levels from commercial ships.

CONCLUSIONS

The results of this study showed that ships within 4 km elevate noise levels by 15–25 dB (10–150 Hz) in the SBC; an elevation in noise of more than 15 dB lasted for approximately 3.1 hours per day, based on the number of ships transiting the channel combined with the average speed of the ships. Compared to another Southern California site that is not exposed to distant shipping and has little local ship traffic, SBC has high sound levels; however compared to the Gulf of Oman, another industrialized site, the sound levels in SBC are only a few dB higher. The impact of these elevated noise levels on the marine ecosystem is still not well understood, but we found that blue whale B calls were not detected when a commercial ship was within 4 km. This suggests that there is a decrease in communication distance for blue whales when a ship is nearby, especially at noon and midnight when ship traffic is the most intense in the SBC.

Current management strategies are focused on the possibility of slowing ships in the channel to reduce noise and decrease the probability of ship strikes. To successfully manage the acoustic impacts on marine mammals from ship noise, managers should define the frequency band for noise level reduction, understand how ship operations may be modified to enact these changes, and understand how marine mammals might benefit from the change.

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SCALES OF VARIABILITY IN LARVAL SETTLEMENT WITHIN THE CHANNEL ISLANDS NATIONAL MARINE SANCTUARY AND ALONG THE MAINLAND COAST

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Abstract—We explored variability in the settlement rates of sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*), and rock crabs (*Cancer spp.*) across different spatial (hundreds of meters to 90 km) and temporal (biweekly to decadal) scales in nearshore waters off Santa Cruz, Santa Rosa, and Anacapa islands and along the Santa Barbara mainland coast. Here, we refer to "settlement" as a best estimate of the abundance of small stages of invertebrates recently settled from the plankton. Settlement was measured using two types of collectors: wood-handled scrub brushes and "tuffy" scrub pads attached 1 to 2 m off the bottom either on buoyed mooring lines at stations inside and outside of two marine protected areas (MPAs) at the islands or suspended from piers, one of which is located inside an MPA at Anacapa Island. Benthic recruitment of urchins was also measured at the Anacapa Island station. Larval settlement varied dramatically on a scale of hundreds of meters within and across MPA boundaries. For both red and purple urchins, average settlement at the Santa Cruz and Santa Rosa island sites in 2006 was an order of magnitude higher than average settlement at mainland sites in 2006 and also higher than the historical mainland average (based on a 16-year time series). Comparisons of settlement relative to benthic recruitment at the Anacapa Island station were suggestive of a link for red urchins, but no relationship was evident for purple urchins. Although more data are needed, our results suggest that local and regional scale variability in larval settlement could have important implications for population dynamics, fishery management, MPAs and sampling design. For example, areas with lower settlement rates may take longer to recover depleted populations or be less suitable for restoration efforts based on natural replenishment than areas with greater settlement. Settlement data could provide a fishery-independent measure of stock health and a means for evaluating the role of larval supply in regulating adult populations of economically and ecologically valuable benthic invertebrates.

INTRODUCTION

Shallow rocky reefs are critically important nearshore coastal ecosystems in southern California. These ecosystems support giant kelp (*Macrocystis pyrifera*), understory macroalgae, seagrasses, and populations of ecologically, commercially, and recreationally important fishes and invertebrates. Many of the benthic invertebrate species of rocky reef ecosystems (e.g., sea urchins, rock crabs) have a distinctive two phase life cycle, with a planktonic larval phase and a benthic adult phase. For those species with a larval phase of short duration, most larvae may be retained in the vicinity of the source adult population; however, as the larval phase increases in duration, there can be extensive dispersal of larvae by currents away from the source adults (see reviews by Morgan 2001; Underwood and Keough 2001; Mitarai et al. 2008). For example, red and purple sea urchin adults are sedentary and likely move no more than a few kilometers and as little as tens to hundreds of meters during a lifetime. In contrast, larvae of these species remain in the plankton for several weeks (Strathmann 1978; Cameron and Schroeter 1980) and may be carried hundreds or thousands of

kilometers from their source population before settlement (Ebert et al. 1994; Miller and Emlet 1997). One consequence of this two-phase life cycle is that the availability of settlers is a potential driver of the dynamics of benthic invertebrate populations and communities along with larval behavior, habitat quality, and post-settlement mortality (e.g., Connell 1985; Roughgarden et al. 1987; Raimondi 1990; Morgan et al. 2000).

The two-phase life cycle of many benthic invertebrates has implications for managing reef populations inside marine protected areas (MPAs) at the Channel Islands and elsewhere. Benthic adult populations inside and outside of MPAs are potentially linked through the passive transport of planktonic larvae by ocean currents (Shanks et al. 2003). Since larvae may spend days to weeks feeding in the plankton, larvae produced by benthic adults within an MPA probably recruit to populations at distance from the MPA. Conversely, populations of these species within an MPA may be maintained by larvae produced outside of the MPA. In addition, settlement rates can vary among different species, affecting the recovery time and resilience of benthic populations. Information on spatial and temporal variation in larval settlement is needed to better understand the factors responsible for regulating the distribution and abundance of benthic invertebrates and to evaluate the potential efficacy of MPAs.

Larval settlement of sea urchins has been monitored at a number of locations in southern and northern California since 1990 (Ebert et al. 1994; Schroeter and Dixon 2006), but few data are available from the Channel Islands. Data from a single station (Landing Cove) on Anacapa Island indicates that sea urchin (*Strongylocentrotus* spp.) settlement occurs primarily from March through September (Schroeter and Dixon 2006). Although there is very little information on settlement for rock crab populations (CDFG 2004), Page et al. (1999) documented benthic recruitment of brown rock crabs (*Cancer antennarius*) into a subtidal mussel community during the late spring and early summer on an offshore oil platform 4.7 km from Ellwood Pier in Goleta.

In this study, we compared the settlement rates of reef invertebrates across various spatial and temporal scales. Here, we refer to "settlement" as a best estimate of the abundance of small benthic stages recently settled from the plankton. Settlement may be a proxy for "larval supply" or the abundance of pre-settlement larvae in the plankton (Miller and Emlet 1997). Specifically, we explored variability in settlement: 1) at three spatial scales ranging from comparisons among stations within (hundreds of meters) and across (<1 to 10 km) MPA boundaries to stations at the Channel Islands versus the mainland (48–94 km); 2) across temporal scales ranging from biweekly to decadal; 3) among species; and 4) relative to benthic recruitment of young-of-year sea urchins (which is likely affected by post-settlement mortality) at a single station located within an MPA. We targeted benthic invertebrate species of commercial and ecological importance: purple and red sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*) and brown and red rock crabs (*Cancer antennarius, C. productus*).

MATERIALS AND METHODS

Study Design and Sampling Sites

We measured spatial and temporal variability in the settlement of red and purple sea urchins and brown and red rock crabs at three spatial scales. At the smallest scale (hundreds of meters to kilometers), settlement was compared among four stations each at Santa Cruz Island (SCI) and Santa Rosa Island (SRI) from May through September 2006 (Fig. 1). At SCI, two stations were located inside and two outside of the Gull Island MPA. At SRI, two stations were located inside and two outside of the Skunk Point MPA. At a larger scale for island sites (tens of kilometers), settlement was compared among the SCI and SRI stations and at a single station (Landing Cove) on Anacapa Island (AI), a long-term site that is located inside an MPA (Fig. 1). There were no outside MPA data available for the Anacapa Island station. Finally, during 2006 we compared settlement at our island stations to three mainland stations in the Santa Barbara Channel 50 to 90+ km distant (Gaviota Pier, Ellwood Pier, Stearn's Wharf). We also placed results from the SRI and SCI island stations in the context of results of a much larger regional long-term monitoring program, which has been in place since the early 1990s. This long-term program measures larval settlement from a network of brush

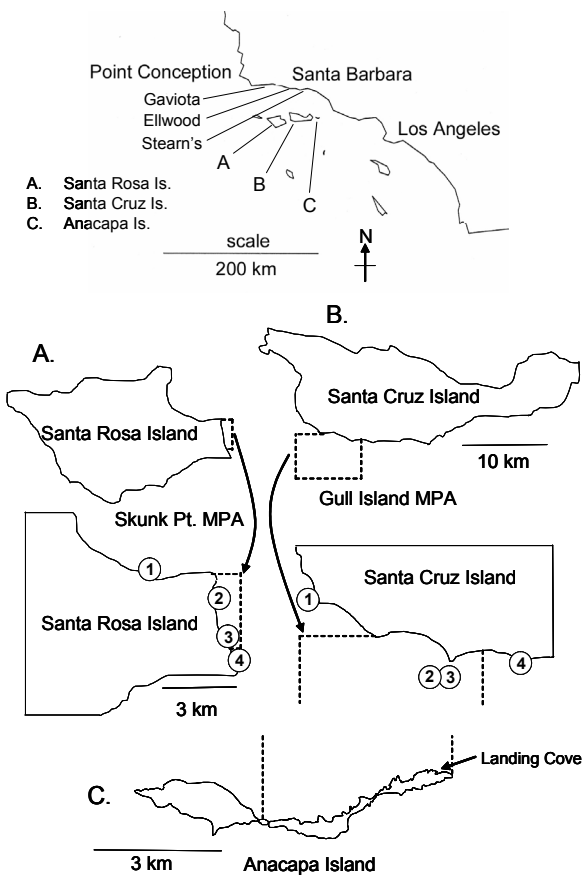

Figure 1. Map showing the location of stations used in the study, including our temporary stations moored inside and outside of A) Skunk Point MPA at Santa Rosa Island (SRI 1-4) and B) Gull Island MPA at Santa Cruz Island (SCI 1-4), and pier stations on the mainland coast and at C) Landing Cove, Anacapa Island. Dashed lines indicate MPA boundaries.

collectors along the mainland coast, including the three stations in the Santa Barbara Channel used in this study (Schroeter et al., unpublished). The sampling station at AI is located ~100 m from a station used by the Channel Islands National Park Service (CINP) to routinely monitor recruitment of selected species of benthic invertebrates (Fig. 1), which is also within the MPA.

Measurement of Settlement and Benthic Recruitment

We measured settlement at SCI and SRI using two types of collectors: wood-handled scrub brushes and "tuffy" scrub pads. At these stations, four brushes and two tuffys were attached to a buoyed mooring line 1 to 2 m off the bottom in 8 to 10 m water depth following the methods of Ebert et al. (1994). Brushes and tuffys were retrieved and replaced using a casing apparatus we developed for this study that allowed surface-based retrieval. Brush and tuffy collectors were retrieved and replaced with fresh collectors at two-week intervals to minimize the potential effects of post-settlement mortality on estimates of settlement. After retrieval, the brushes and tuffys were placed on ice for transport and processing at UCSB following methods in Ebert et al. (1994). The settlement of urchins on brushes and tuffys was highly correlated (total urchins—r^2=0.75, No. tuffy^{-1} = 1.32•(No. brush^{-1}) + 1.86). A similar pattern was found for crabs (total crabs—r^2 = 0.68, No. tuffy^{-1} = 2.76•(No. brush^{-1}) - 0.06); therefore, we present only the data from the brushes here. At the mainland and AI stations, four brushes were attached to a line 1 to 2 m above the bottom suspended from a pier (Schroeter and Dixon 2006).

The relationship between settlement and benthic recruitment was examined at AI using data collected by the CINP from artificial recruitment modules (ARMs). These modules consist of a wire cage made of 5 x 10 cm plastic coated mesh wire filled with 20 bricks made by cutting a concrete cinder block in half longitudinally, which produces two bricks each with a cross section shaped like a lower case "m." The ARMs are taken apart and the animals inside of them (including red and purple sea urchins but not rock crabs) are collected and measured once a year. Between three to seven ARMs were sampled at the Landing Cove site in a given year. Counts of red and purple urchins 30 mm in test diameter, considered to be less than two years old based on previous growth studies (Ebert et al. 1999; CDFG 2004), were used as a measure of recruitment. Comparisons were made for 1994 through 1998, years in which more than 50% of biweekly samples were collected.

Data Analysis

We investigated similarity in patterns of settlement among stations within SCI and SRI, and for grouped stations between these island sites, using Pearson correlation analysis. We compared mean settlement values with ANOVA. In addition, we used commonality analysis to estimate the amount of variability in settlement rates accounted for by three different spatial scales: 1) among

stations within areas (within MPAs or adjacent areas outside of MPAs); 2) between areas (inside versus outside of MPAs); and 3) between islands (Santa Rosa versus Santa Cruz) (Siebold and McPhee 1979; Rowell 1991). We examined the relationship between settlement and recruitment first by plotting yearly averages of recruits per ARM and settlers per brush as a function of year. In addition, we conducted linear regression analysis of recruitment in a given year versus settlement one or two years earlier.

RESULTS

Spatial and Temporal Patterns in Settlement at Island Sites

There was considerable small-scale variability (across hundreds of meters to a few kilometers) in the settlement of purple and red sea urchins and brown rock crabs within sites (Santa Cruz and Santa Rosa islands); there was no settlement of red rock crabs at our island stations during the study. Settlement rates of purple and red urchins and brown rock crabs were generally higher at stations 1 and 4 compared with 2 and 3 at SCI, and stations 2 and 3 compared with 1 and 4 at SRI. No consistent pattern with respect to MPA boundaries was detected in settlement. Variability among stations was particularly noticeable for purple urchins on June 11 at SCI when settler density was 3.1 times higher at station 3 compared to the next highest station (station 4) located 1.5 km distant (Fig. 1).

Although the abundance of purple sea urchin settlers varied among stations at SRI, patterns in settlement were highly correlated among stations over time (Table 1; Fig. 2). However, this correlation was not evident for red urchins or brown rock crabs, both of which exhibited much lower settlement intensity. The temporal correlations observed in settlement among stations were weaker for purple urchins at SCI, with a significant correlation only between SCI stations 2 and 4 (Table 1). No correlations were detected in settlement over time among the SCI and SRI sites for any species (maximum $r^2 = 0.4$). As a consequence of variability in settlement among stations and over time, no significant difference in average settlement was found between SCI and SRI sites ($P > 0.1$).

Commonality analysis indicated that differences among stations (smallest scale) accounted for most of the variation in settlement observed for all three species, followed by differences between SCI and SRI (sites), and finally by status with regard to MPAs (inside versus outside) (Fig. 3).

Settlement at Island and Mainland Sites

In 2006, the settlement of purple urchins was higher on average at SCI and SRI (mean = 1.47 settler brush^{-1} week^{-1}) than at the mainland (mean = 0.22 settler brush^{-1} week^{-1}) or at AI (mean = 0.04

Table 1. Matrices of simple correlation coefficients (r) in pairwise comparisons of larval settlement onto brushes over time between stations at Santa Cruz Island (SCI) and at Santa Rosa Island (SRI) for purple and red urchins and brown rock crab in 2006. Significant correlations indicated with asterisks: *P < 0.05, **< 0.01, ***< 0.001. Missing data indicated by ----.

	SCI 2	SCI 3	SCI 4		SRI 2	SRI 3	SRI 4
			Purple urchin				
SCI 1	-0.281	0.818	0.711	SRI 1	0.833*	0.877**	0.869*
SCI 2		-0.192	0.946**	SRI 2		0.810*	0.745
SCI 3			-----	SRI 3			0.960***
			Red urchin				
SCI 1	-0.409	-0.343	0.793	SRI 1	0.740	0.318	-0.123
SCI 2		-----	0.149	SRI 2		0.925***	0.853*
SCI 3			-----	SRI 3			0.803*
			Brown rock crab				
SCI 1	0.582	-0.812	0.834	SRI 1	0.066	0.417	-0.316
SCI 2		-----	0.333	SRI 2		0.524	-0.050
SCI 3			-----	SRI 3			-0.03

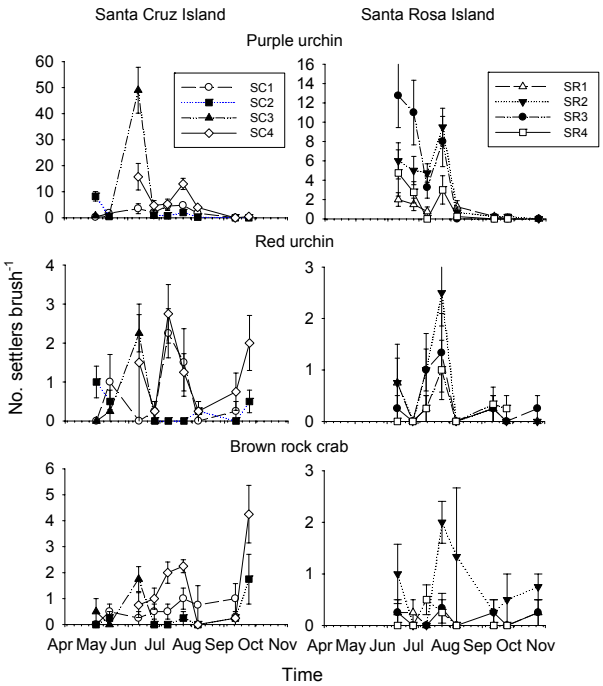

Figure 2. Settlement of purple and red sea urchins and brown rock crabs onto brush collectors sampled at approximately two-week intervals at stations nearshore of Santa Rosa and Santa Cruz islands. Open symbols are data for station located outside MPAs and closed symbols are for station located inside MPAs. Note differences in scale of the y-axis among figures.

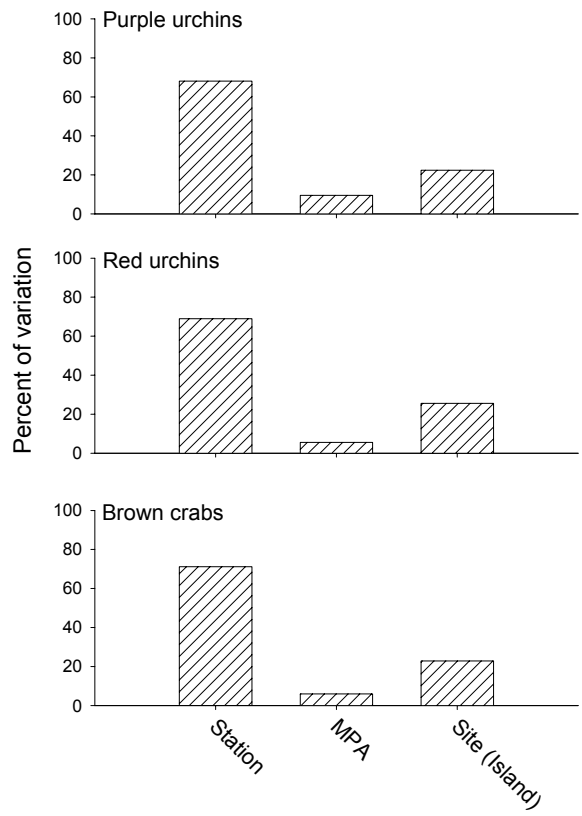

Figure 3. Percent of variation in settlement on the brushes attributable to differences among stations, stations inside and outside of MPAs, and sites (island versus mainland).

settler brush^{-1} week^{-1}) (Fig. 4). Similarly, settlement of red urchins was higher at SCI and SRI (mean = 0.22 settler brush^{-1} week^{-1}) than at the mainland (mean = 0.03 settler brush^{-1} week^{-1}) or at AI (mean = 0.01 settler brush^{-1} week^{-1}). However, there was no difference in settlement of brown rock crabs between SCI and SRI (mean = 0.10 settler brush $^{-1}$ week^{-1}) and the mainland (mean = 0.10 settler brush^{-1} week^{-1}). Settlement of brown rock crabs at AI (mean=0.03 settler brush $^{-1}$ week^{-1}) was lower than at SCI, SRI, or the mainland. Settlement of red rock crabs occurred only at our mainland stations and was very low.

Examining our data from 2006 within the context of the 16-year data set, indicates that relative settlement between the island and mainland sites varied among three of the four target species. Settlement of red rock crabs, which was very low at the mainland stations, was not considered. Settlement of purple urchins at mainland and AI stations was generally much lower in 2006 compared to the long-term average settlement at those stations, and this was the trend as well on SCI and SRI with the exception of stations 3 and 4 on SCI (Fig. 4). The patterns of settlement were very different for red urchins, where settlement at the AI and mainland stations in 2006 was either lower or similar to long-term averages. However, the 2006 settlement at SCI and SRI stations (with the exception of station 1 on SRI) was generally much higher than the long-term averages at mainland and AI stations (Fig. 4). With a single possible exception of station 4 on SCI, brown rock crab settlement on SCI and SRI was either similar to or lower than the long-term averages at the mainland and AI stations (Fig. 4).

Settlement versus Benthic Recruitment

We explored the relationship between settlement and recruitment into the benthic population using data from 1994 through 1998 on the availability of settlers from the brushes and the

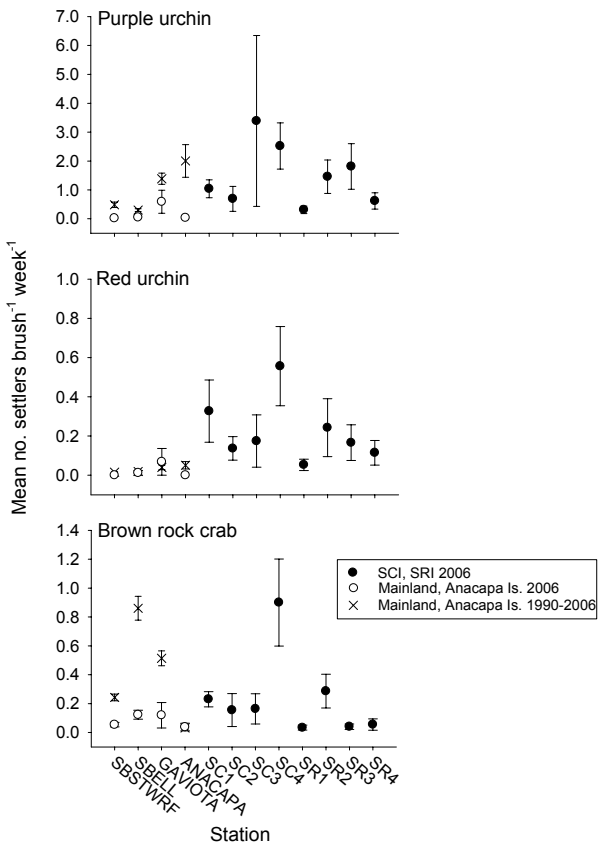

Figure 4. Comparison of settlement rate of purple and red urchins and brown rock crab onto brush collectors among island and mainland stations in 2006, between SCI and SRI stations in 2006 and historical data from Anacapa Island and the mainland averaged from 1990 through 2006. Note differences in scale of the y-axis among figures.

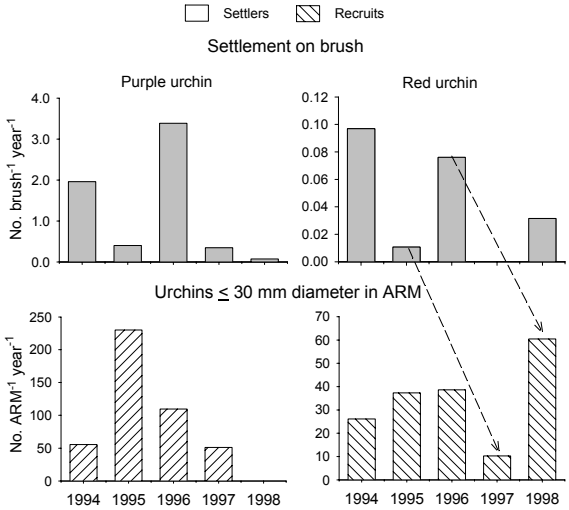

Figure 5. Relationship between the mean number of urchin settlers on the brush collectors and the number of urchins < 30 mm in the ARMs at the Landing Cove station on Anacapa Island, 1994 through 1998. Note differences in scale of the y-axis among figures. Arrows indicate two year time lag between settlement and benthic recruitment for red urchins.

abundance of purple and red urchins ≤ 30 mm diameter in the ARMs located at the Landing Cove station on AI (Fig. 5). Growth of purple and red urchins following settlement is reported to range from ~10 to 30 mm in one year (Ebert 1968; Kenner 1992; Ebert et al. 1999); therefore, an urchin of ≤ 30 mm likely recruited into the benthic population within the previous 1 to 2 years. To account for variability in growth and settlement, time lags of 1 and 2 years were used to explore relationships between settlement and benthic recruitment.

For purple urchins, there was no relationship between settlement on the brushes and the abundance of urchins ≤ 30 mm in the ARMs at time lags of either 1 ($r^2 = 0.02$) or 2 years ($r^2 = 0.10$) (Fig. 5). For red urchins, there was also no relationship between settlement and the abundance of urchins ≤ 30 mm at a time lag of 1 year ($r^2 = 0.42$); however, there was a positive relationship ($r^2 = 0.60$) between settlement and the abundance of urchins ≤ 30 mm with a time lag of 2 years (Fig. 5).

DISCUSSION

The abundance of settling larvae can strongly influence benthic recruitment and the dynamics of marine invertebrate populations (reviews by Morgan 2001; Underwood and Keough 2001; Wahle 2003). The spatial scale across which settlement rate varies may thus have important implications to the sustainability of populations and their rate of recovery following a disturbance. Much of the work on spatial variation in settlement has centered on intertidal species, particularly barnacles and mussels, which are amenable to sampling and experimental manipulation (e.g., Connell 1985; Raimondi 1990; McQuaid and Phillips 2006). Our study shows that for two urchin and one crab species, settlement rates can vary appreciably across spatial scales on the order of hundreds of meters (station scale) to tens of kilometers (Island/Mainland scale). We also found significant

temporal variation in settlement across our shortest (biweekly) time scale and among years.

Although absolute settlement rates varied among stations and over time, correlation analysis revealed coherence in the temporal patterns of settlement for purple and red urchins among some stations, most notably at SRI. However, on SCI the timing of settlement peaks generally differed among stations, some of which were quite close spatially (< 500 m: Fig. 1). Oceanographic conditions, such as the direction and speed of prevailing alongshore currents and upwelling, which influence cross shelf transport, can regulate larval supply and the magnitude and timing of settlement across large spatial scales (e.g., Roughgarden et al. 1987; Gaines and Bertness 1992; Miller and Emlet 1997; Shanks and Roegner 2007). These larger scale oceanographic conditions, which differ between the northern Channel Islands and mainland (Otero and Siegel 2004), could have contributed to the dramatically lower settlement of urchins observed at AI, and our two most easterly mainland stations, compared to SRI and SCI in 2006 and relative to the 16-year average. However, if such a large-scale current pattern were important, one would expect to see similar patterns among the three species (whose larvae have similar planktonic duration) over the long term. This was clearly not the case, as the spatial pattern in 2006 and long-term averages were similar for red sea urchins (indicating a west to east decline in settlement rates) but not for purple urchins and brown rock crabs. For these species the long-term settlement at AI and two mainland stations was either similar to or exceeded settlement at SCI and SRI, and differed from the patterns seen for red sea urchins. Our findings suggest that hydrographic conditions that modulate larval delivery to subtidal reefs at much smaller spatial scales (e.g., local eddies or variability in water flow created by bottom topography) may be as or more important than large-scale current patterns.

Of potentially greater importance to benthic populations is the total number of settlers that arrive on a reef during the year. Annual variability in settlement could influence benthic recruitment and ultimately the abundance of adults within a year class. Such population level effects were postulated to occur following unusually high settlement rates of red urchins in northern California after the 1992 and 1993 El Niño events (Ebert et al. 1994; Morgan et al. 2001; Schroeter and Dixon 2006). The absence of a correlation between settlement and benthic recruitment would suggest the importance of early post-settlement mortality (e.g., from predation) in limiting recruitment. Because continuous data were available for only a few years, we were unable to adequately characterize the relationship between the availability of settlers (as measured by settlement on brushes) and the abundance of benthic recruits (as measured in the ARMs) from the Landing Cove station on Anacapa Island. Our data are suggestive of a link between settlement and recruitment for red urchins, a harvested species, but no relationship was evident for purple urchins which are not harvested. A longer time series is needed to better evaluate the importance of pre- and post-settlement processes to the population dynamics of purple and red urchins in the Santa Barbara Channel.

It is important to note that our study focused on spatial and temporal patterns of settlement as a proxy for larval supply, and for sea urchins, on the possible effects of this variability on abundances of 1- to 2-year-old recruits. We did not examine possible stock-recruitment relationships for several reasons. First, the data on abundance of adult stocks of the target species are lacking from most of our study sites. Second, while the spatial scales we examined allow a comparison of settlement rates inside and outside of MPAs, our work focused on variations of larval inputs to MPAs rather than the possible effects of MPAs on larval supply. There are at least two reasons for this. First and foremost, even if MPAs affect stocks and ultimately the larval supply, our study was conducted too soon after MPA establishment to detect any possible effects. Second, all of our target species have long-lived (> 3 weeks to months) planktonic larvae, making the detection of any stock-to-recruitment signal problematic.

Variability in settlement within and/or between sites poses problems for making comparisons of annual settlement among, for example, spatial gradients from the inside to the outside of an MPA or among MPAs. This is dramatically illustrated by our data from station SC3 inside of Gull Island MPA. During our study most of the settlement occurred in a single sample date in June 2006 (Fig. 2). We did not anticipate this high station-to-station asynchrony in settlement, as previous studies found

relatively high station-to-station synchrony among even more widely spaced stations (Ebert et al. 1994; Schroeter and Dixon 2006). Understanding the degree of synchrony in settlement is important to the design of monitoring programs (e.g., determining how many study sites to include in a program). Even though our study was unable to provide an estimate of the number of stations necessary to adequately estimate differences in settlement inside and outside of MPAs, the results indicate that single stations are certainly insufficient and could result in an under- or overestimate of yearly settlement within a particular area.

Our results indicate that some areas may consistently experience low larval settlement, which may have important implications for evaluating the performance of MPAs as well as various management actions. Stations receiving much lower larval supplies may take longer to recover depleted populations, or be less suitable for restoration efforts based on natural replenishment, than areas with greater settlement. Thus, data on settlement rates can serve as important covariates in evaluating the performance of MPAs (or other management practices), allowing sites to be compared based on the magnitude of larval input.

Finally, studies of settlement rates can be useful in fisheries management. To our knowledge, the management of nearshore invertebrate fisheries in California relies almost exclusively on fishery-dependent data (e.g., harvest in pounds, species landed, fishing effort, individual size, and sex ratio measurements). Settlement data provide a fishery-independent measure of stock health and a means for evaluating the role of larval supply in regulating adult populations of economically and ecologically valuable benthic invertebrates. Maintaining a long-term data set on settlement and oceanographic conditions also provides a robust measure of stock condition in the face of changes in large scale, long-term oceanographic-related features and climate.

In conclusion, despite the seemingly extensive design suggested by results of the present study (i.e., unbroken strings of biweekly sampling at all sites of potential interest), we argue that monitoring settlement can be both an informative and cost-effective approach to acquiring estimates of stock condition and evaluating MPAs. While many sampling events are required, each event requires relatively little effort. We have maintained such a design for 14–16 years as proof of the feasibility of our approach. A key element in maintaining the scope of such a study has been the participation of fishing partners for both funding and in-kind support.

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SPATIAL PATTERNS OF INTERTIDAL COMMUNITY STRUCTURE ACROSS THE CALIFORNIA CHANNEL ISLANDS AND LINKS TO OCEAN TEMPERATURE

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Abstract—We evaluated the spatial patterns in rocky intertidal community structure through surveys of rocky intertidal communities at the California Channel Islands. We sampled (22) sites spread across 7 California Channel Islands: San Miguel (2), Santa Rosa (5), Santa Cruz (6), Anacapa (3), San Nicolas (2), Santa Barbara (2), and Santa Catalina (2) over a five-year period from 2001 to 2006. We used non-metric multidimensional scaling analyses to examine spatial patterns of community similarity among island sites. We found strong evidence for spatial variation in community similarity across the islands. Sites on Santa Catalina Island were most similar to each other and had very little similarity to all other island sites. In some cases, nearby sites within the remaining six islands formed groups most similar to each other; however, in many cases similarity was higher among distant sites than among sites on the same island. Nearshore oceanographic conditions, as indexed by sea surface temperature (SST), were highly correlated to the overall pattern of community similarity. Similar to findings from a smaller-scale study at Santa Cruz Island, we observed strong associations between SST and patterns of community structure. Invertebrate abundance was highly correlated with SST across all sites, while macrophyte abundance showed the opposite response. The spatial patterns of community similarity found here and the strong links to ocean temperature are strikingly similar to those recently described for intertidal communities along the mainland Pacific coast of North America and the coast of Chile. We suggest that similar oceanographic dynamics and ecological interactions may drive patterns of community structure across these large spatial scales.

INTRODUCTION

A major goal of ecology is to understand the factors contributing to the distribution and abundance of organisms at a variety of spatial scales. As broad scale questions are increasingly dominant in conservation and management, marine ecologists have been pressed to examine linkages between patterns and processes operating at spatial scales larger than individual sites (Dayton and Tegner 1984; Polis and Hurd 1996; Schiel et al. 2004; Schoch et al. 2006). In marine systems, this 'scaling-up' has resulted in a significant conceptual shift in our understanding of the connections among populations and communities and the importance of benthic–pelagic linkages. Benthic communities are inextricably linked to the oceanic environment through the delivery of food, nutrients, propagules, and larvae. The oceanographic processes driving the delivery of these constituents span large spatial scales and thereby connect distant onshore communities (Gaines et al. 1985; Roughgarden et al. 1988; Bustamante et al. 1995; Menge et al. 1997b; Schiel 2004).

Recent ecological studies from eastern boundary upwelling ecosystems around the world support a strong coupling between coastal oceanography and nearshore benthic community structure. In South Africa, it has been established that large-scale patterns of nearshore community structure covary with gradients of productivity and wave exposure (Bustamante and Branch 1996). Along the coast of Chile, several studies provide evidence that oceanographic variability is strongly correlated with the abundance of dominant intertidal functional groups (Broitman et al. 2001; Nielsen and Navarrete 2004). Around New Zealand, rocky intertidal structure and dynamics vary with

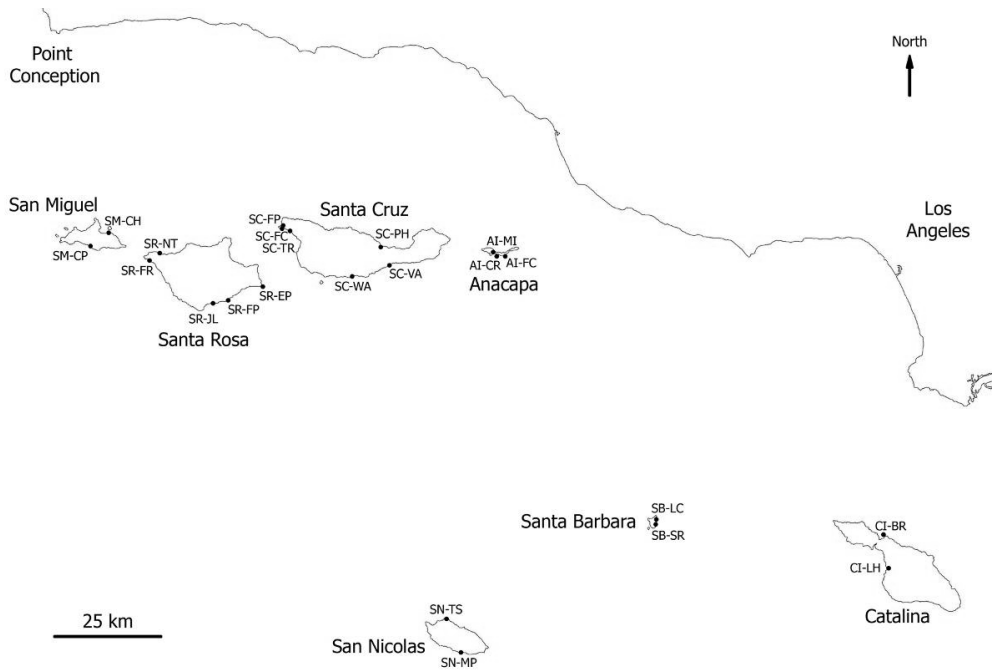

Figure 1. Map showing locations of Channel Islands rocky intertidal sites. Site codes are as listed in Table 1.

large-scale oceanographic conditions in nearshore environments (Menge et al. 1999, 2003). On the U.S. west coast, nearshore oceanographic conditions have been shown to determine community structure along the coast of Oregon (Menge et al. 1997a, b) and more recently, along the entire Pacific coast of North America (Blanchette et al. 2008).

Along the U.S. Pacific coast, two major water masses meet at Point Conception, California—the southward flowing California current, and the westward flowing southern California countercurrent (Hickey 1993). This region is one of the most important biogeographic and oceanographic discontinuities on the west coast of North America (Valentine 1966; Doyle 1985; Burton 1998). The northern region is typified by consistently strong coastal upwelling bringing cold, nutrient-rich waters to the surface, resulting in both cold sea surface temperatures along the coast and high nutrient concentrations. The Santa Barbara Channel, immediately south/east of Point Conception, is typified by weak seasonal upwelling, which tends to occur in the winter months (Blanchette et al. 2002; Winant et al. 2003). The California Channel Islands are located just offshore from Point Conception and lie within this highly diverse oceanographic region (see Fig. 1). The broad range of sea surface temperatures and oceanographic variability found across the entire Point Conception region are found at a much smaller geographic scale within this island group (see Fig. 2). These islands experience variable mixing between the cold waters of the California current and the warm, nearshore waters of the southern California countercurrent (Huyer 1983; Hickey et al. 2003).

The Channel Islands are known to contain an incredibly diverse assemblage of marine species (Neushul et al. 1967; Murray and Littler 1981). This great diversity is due largely to: 1) their location near the boundary of two major biogeographic provinces (the Oregonian and the Californian); 2) their diversity of habitat types and exposure to varying oceanographic conditions; and 3) their high productivity resulting from upwelling of cold nutrient-rich water off Point Conception. Oceanographic conditions are known to strongly influence the structure of nearshore biological communities via delivery of nutrients and larvae, and direct influences on growth, productivity, and reproduction. Ocean temperature is probably one of the best single correlates of environmental variability in the nearshore environment in cold-

temperate regions of the world. Low ocean temperatures at the mesoscale are associated with nutrient influx and increase abundance of primary producers (Nielsen and Navarrete 2004; Broitman and Kinlan 2006). In contrast, elevated temperatures have also been shown to affect rates of foraging and growth (Sanford 2002; Blanchette et al. 2007). Increased temperature is also associated with ocean circulation patterns favoring larval delivery and invertebrate recruitment (Connolly et al. 2001; Broitman et al. 2008).

The biogeographical significance of the exposure of the Channel Islands to different oceanographic temperature regimes was recognized early by Hewatt (1946), who was among the first to describe the marine invertebrate faunas around Santa Cruz Island and their intermediate biogeographical affinities with the faunal elements characteristic of mainland habitats north and south of Point Conception. Although this early documentation was mainly descriptive and contains only single point measures of seawater temperature, Hewatt (1946) noted the potential importance of ocean temperature differences across the island to variability in community patterns around the island. More recently, we found that the structure of intertidal communities around Santa Cruz Island was strongly linked to oceanographic conditions as indexed by long-term mean ocean temperature (Blanchette et al. 2006). Warmer temperatures were associated with invertebrate-dominated sites and high invertebrate recruitment (Broitman et al. 2005). Cooler temperatures were associated with macrophyte-dominated sites with high algal growth and productivity and reduced invertebrate growth, similar to findings from a range of sites spanning a similar oceanographic gradient around Point Conception (Blanchette and Gaines 2007; Blanchette et al. 2007).

The location of the California Channel Islands provides a unique opportunity to examine the relationship between nearshore oceanographic conditions and biological community structure across a relatively small spatial scale. Here we describe the biogeographic patterns of intertidal rocky shores across the California Channel Islands and examine patterns of species similarity relative to both geographic distance and oceanographic conditions.

MATERIALS AND METHODS

Study Region and Biological Sampling Design

We conducted quantitative surveys at 22 rocky intertidal sites distributed across 7 California Channel Islands—San Miguel, Santa Rosa, Santa Cruz, Anacapa, San Nicolas, Santa Barbara and Santa Catalina—over a 5-year period from January 2001 to January 2006. (Fig. 1; Table 1). These sites were all gently sloping (0°–20°) rocky benches and were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type (see Blanchette et al. 2008 for more detail). Sites were chosen based on accessibility and to be generally representative of the intertidal flora and fauna of that island region. Sites were also chosen to overlap with existing data collection efforts by several major research groups (PISCO, MARINe, and CINP).

We used a stratified point-intercept sampling method to quantify percentage cover of sessile invertebrate and macrophyte species at each site. A representative shore section 30 m long was designated as the site. A 30-m baseline tape was laid out along the upper edge of the highest intertidal barnacle zone, parallel to the shore. A point-intercept transect was then surveyed perpendicular to the horizontal tape at each 3-m interval, for a total of 11 transects per site. These vertical transects extended from the upper edge of the barnacle zone to about the 0.0 m MLLW level predicted by the tide

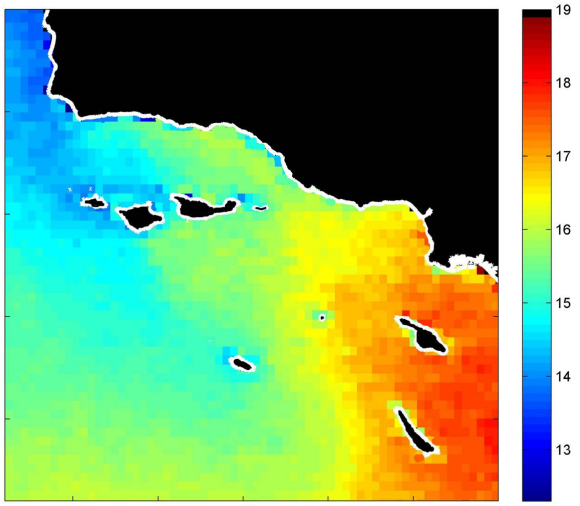

Figure 2. Long-term mean Advanced Very High Resolution Radiometer Sea Surface Temperature (AVHRR SST) from 1996 to 2005.

Table 1 . Characteristic taxa (top 10) for each of the island site groups shown in Figure 4 as determined by SIMPER analysis. The ranking is determined by S_i, the average contribution of each species to the overall similarity of the zone in each region. %Av indicates the average percentage cover of each species from all sites. $\Sigma\%S_i$ is the cumulative percentage contribution of each species to the overall average similarity (S).

Characteristic taxa	%Av	S_i	$\Sigma\%S_i$
Group 1 – green (S = 72.16)			
Littorina keenae	0.79	8.98	12.44
Bare rock	0.5	5.72	20.36
Lottia scabra/conus	0.32	3.23	24.84
Corallina spp	0.26	2.47	28.27
Phyllospadix torreyi	0.25	2.39	31.59
Chondracanthus canaliculatus	0.25	2.35	34.85
Littorina plena/scutulata	0.24	2.24	37.96
Endocladia muricata	0.2	2.23	41.05
Phragmatopoma californica	0.24	2.2	44.1
Lottia paradigitalis/strigatella	0.21	2.11	47.03
Group 2 – blue (S = 65.32)			
Bare rock	0.54	5.57	8.53
Littorina keenae	0.53	5.41	16.81
Lottia austrodigitalis/digitalis	0.41	4.11	23.09
Lottia scabra/conus	0.3	3.14	27.9
Phragmatopoma californica	0.28	2.96	32.43
Corallina spp	0.27	2.86	36.81
Lottia paradigitalis/strigatella	0.2	2.13	40.07
Littorina spp	0.32	1.95	43.05
Chondracanthus canaliculatus	0.22	1.92	45.98
Littorina plena/scutulata	0.23	1.91	48.91
Group 3 – yellow (S =71.96)			
Littorina keenae	0.78	9.87	13.71
Bare rock	0.48	5.15	20.86
Mytilus californianus	0.35	3.73	26.04
Chthamalus spp	0.3	3.71	31.21
Corallina spp	0.29	3.53	36.12
Littorina plena/scutulata	0.29	3.49	40.97
Encrusting coralline	0.29	3.12	45.3
Lottia scabra/conus	0.24	2.85	49.26
Tetraclita rubescens	0.21	2.31	52.47
Halidrys dioica	0.19	2.11	55.39
Group 4 – purple (S = 72.55)			
Littorina keenae	0.88	11.81	16.28
Bare rock	0.39	4.69	22.75
Littorina plena/scutulata	0.32	3.89	28.1

Table 1 (continued). Characteristic taxa (top 10) for each of the island site groups shown in Figure 4 as determined by SIMPER analysis. The ranking is determined by S_i, the average contribution of each species to the overall similarity of the zone in each region. %Av indicates the average percentage cover of each species from all sites. $\Sigma\%S_i$ is the cumulative percentage contribution of each species to the overall average similarity (S).

Characteristic taxa	%Av	S_i	$\Sigma\%S_i$
Chondracanthus canaliculatus	0.29	3.25	32.58
Chthamalus spp	0.27	3.14	36.91
Endocladia muricata	0.22	2.81	40.78
Lottia scabra/conus	0.19	2.16	43.76
Mazzaella affinis	0.16	2.05	46.59
Silvetia compressa	0.19	1.89	49.19
Balanus glandula	0.12	1.57	51.35
Group 5 – orange (S = 72.20)			
Littorina keenae	0.78	8.97	12.42
Mytilus californianus	0.48	5.48	20
Bare rock	0.5	5.32	27.37
Lottia scabra/conus	0.31	3.62	32.39
Corallina spp	0.29	3.04	36.6
Tetraclita rubescens	0.2	2.1	39.51
Lottia pelta	0.23	1.98	42.25
Mazzaella affinis	0.17	1.92	44.9
Chthamalus spp	0.16	1.7	47.26
Lottia paradigitalis/strigatella	0.17	1.65	49.55
Group 6 – red (S = 65.61)			
Littorina keenae	0.78	7.17	10.93
Bare rock	0.4	3.8	16.72
Littorina plena/scutulata	0.33	2.85	21.07
Halidrys dioica	0.27	2.76	25.27
Tetraclita rubescens	0.24	2.45	29.01
Corallina spp	0.29	2.43	32.72
Chondracanthus canaliculatus	0.24	2.38	36.34
Silvetia compressa	0.24	2.11	39.56
Lottia scabra/conus	0.28	1.97	42.55
Chthamalus spp	0.25	1.76	45.23

tables (generally the surfgrass zone). Along each vertical transect the species or taxon located under each point at a pre-determined interval along the tape was scored sequentially. The distance between transects at each site depended on the size and topography of the bench and was calculated to provide at least 100 points sampling points per transect. For example, if a vertical transect extended 20 m, the sampling interval would be 20 cm. For each point, we sampled the taxa directly under the point, then additionally the two nearest taxa within a radius equivalent to half the sampling interval from that point. Percentage cover estimates reported here are based on the primary taxa attached to rock located directly under each point.

Mobile invertebrate taxa (e.g., limpets, snails, whelks) were scored by direct counts within 33 0.25-m^2 quadrats along each of the vertical

transects. At each transect, the vertical distribution of high, mid, and low zones were assessed visually, and quadrats were randomly placed within each of these zones. Because the predatory seastar (*Pisaster ochraceus*) is much larger than most other intertidal invertebrates, and primarily occurs in channels and crevices, we counted the number of seastars within a 2-m swath centered along each of 11 vertical transects.

Sea Surface Temperature Analyses

We followed the approach of Broitman et al. (2005) and Blanchette et al. (2006) and characterized oceanographic conditions at each site through spatial and temporal patterns of sea surface temperature (SST) from the Advanced Very-High Resolution Radiometer (AVHRR) of a nominal resolution of 1.1 km averaged over 5 days. From the AVHRR dataset we selected the pixels corresponding to the locations of our 22 intertidal sites and averaged the first three cross-shelf pixels since missing pixels were common in the nearshore. Long-term means were derived directly from the resulting time series from 1996 through 2005 (Fig. 2). We chose to use satellite-based SST for this analysis due to the availability of long-term data for all of our study locations. One of the great advantages of using remotely sensed observations is that one can explore biophysical relationships in many parts of the world where satellite-based data are available, but long-term data from in-situ physical instrumentation are not. Long-term satellite data also provide a much better index of the persistence of oceanographic regimes over the extended periods of time and across broad spatial scales.

Data Analysis

To examine geographic patterns of community similarity, we used the multivariate methods of Clarke (1993) and the PRIMER 6.1.3 (Plymouth Routines in Multivariate Ecological Research) software package. The data matrix of taxon abundances was square root transformed to reduce the contribution of very abundant species and increase that of rare species. A similarity matrix was constructed using the Bray-Curtis similarity coefficient, and cluster analysis was performed using a hierarchical method with group-average linking. We used two-dimensional, non-metric multidimensional scaling (nMDS) to examine regional segregation among communities (Kruskal and Wish 1978). A SIMPROF test using 10,000 permutations was run for the dendrogram to indicate significant group structure at the 0.1% level. For sites sampled in multiple years, we found temporal variability in community structure to be extremely small relative to spatial differences among sites. Based on these findings and in order to focus on spatial patterns, we averaged species abundances across sampling years for all sites. For those groups that differed significantly based on the SIMPROF test, characteristic taxa were then identified using similarity percentage breakdown analyses (SIMPER).

We used Mantel tests to examine the correlation between the matrices of community similarity and coastal distances among sites and differences in long-term mean SST among sites (Legendre 1993; Legendre and Legendre 1998; Legendre et al. 2005). The results of these analyses enabled us to test the prediction that community similarity is correlated with both geographic distance and oceanographic climate (Blanchette et al. 2008). However, two variables may appear to be correlated simply because they are both linked to a third, common variable, such as location in space. Thus, in the presence of autocorrelation, it is necessary to remove the effect of this third variable before concluding that the original two variables are indeed correlated, similarly to a partial correlation. This can be done with the partial Mantel test (Smouse et al. 1986; Legendre and Troussellier 1988; Fortin and Payette 2002). A significant coefficient of correlation (r) for the partial Mantel test (with spatial effects removed) indicates that the relationship that exists between the two variables is not related to a common spatial structure (Legendre and Fortin 1989). We used a partial Mantel test to examine the correlation between community similarity and SST while controlling for the effects of geographic location. The Mantel and partial Mantel tests were based on 10,000 random permutations with a Pearson correlation coefficient at a significance level of α=0.05. All Mantel tests were done using zt software (Bonnet and Van de Peer 2002).

RESULTS

Cluster Analysis and Non-Metric Multidimensional Scaling

Hierarchical cluster analysis and two-dimensional nMDS ordination were used to explore community similarity among sites across the Channel Islands. The two-dimensional structure among sites and the relative spatial separation among sites coded by islands are revealed in the nMDS plot (Fig. 3). Sites located on the same island sometimes cluster close together; however, there is a high degree of scatter among same-island sites. The nMDS is useful for determining which sites form the most cohesive groups (e.g., sites CI-BR and CI-LH). The general geographic configuration of sites from northwest to southeast is apparent in the nMDS plot, going from left (northwestern sites) to right (southeastern sites). The dendrogram illustrates the spatial patterns of island site groupings (Fig. 4). The SIMPROF test identified 6 significantly different groups of sites and 4 sites (sites SR-NT, SM-CP, SR-EP, and SC-PH) as outliers. Apart from these outliers, groups of sites generally corresponded to the spatial pattern of ocean temperature, and did not cluster by island (Fig. 5).

Characteristic Taxa

Characteristic taxa for each of the island groups are shown in Table 1. The cold water sites of San Miguel, Santa Rosa, San Nicolas and western Santa Cruz Island (blue and green groups) were characterized by relatively high abundance of the seaweeds *Chondracanthus canaliculatus, Endocladia muricata*, coralline algae, the surfgrass *Phyllospadix torreyi* as well as the colonial tubeworm, *Phragmatopoma californica* and the limpets *Lottia scabra* and *L. conus*. Warm water sites at Catalina and Santa Barbara Island (orange and red groups) were characterized by relatively high abundance of the mussel, *Mytilus*

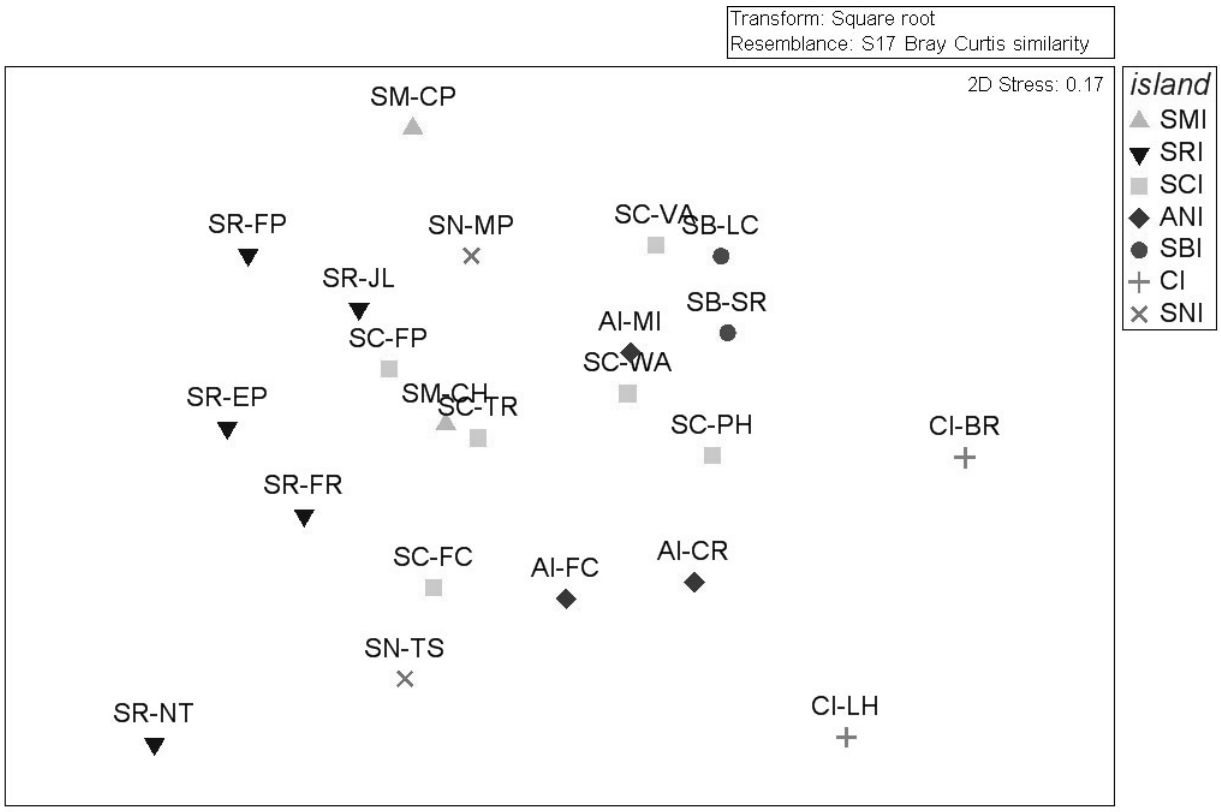

Figure 3. Non-metric multidimensional ordination plot (stress=0.17) using Bray-Curtis similarity based on the square-root transformed taxon abundance data for each of the 22 sites across the 7 islands.

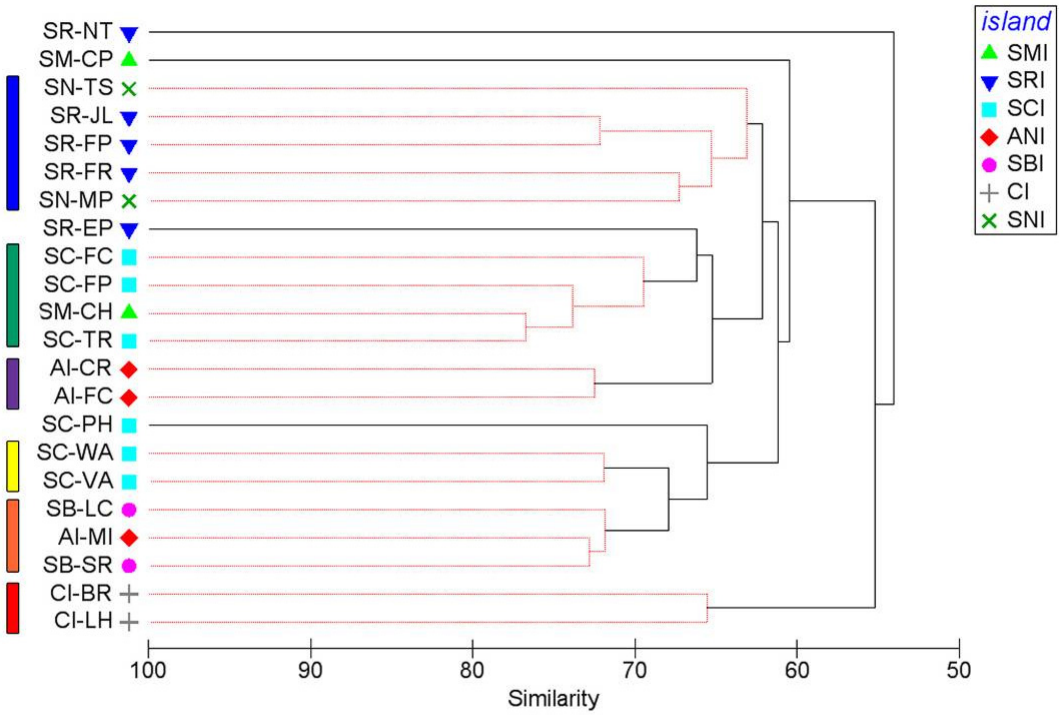

Figure 4. Dendrogram depicting Bray-Curtis similarity in species composition among island sites. Islands are coded by colored symbols. Solid lines indicate significant group structure at the 0.1% level. Color bars to the left of site codes indicate the clusters of sites represented in each of the 6 groups (Group 1 – green, Group 2 – blue, Group 3 – yellow, Group 4 – purple, Group 5 – orange, Group 6 – red).

californianus, the barnacles *Tetraclita rubescens* and *Chthamalus* spp., and the seaweeds *Halidrys dioica* and *Silvetia compressa*. The geographical and thermal 'intermediate' site groups at southern Santa Cruz Island and Anacapa Island (purple and yellow groups) were characterized by a mixture of taxa from both the colder and warmer regions (Table 1).

Geographic and Environmental Correlates of Community Similarity

We used the Mantel and partial Mantel tests to explore the relationships between community similarity and geographic distance and ocean conditions. Community similarity among sites decreased significantly with geographical distance (Mantel r=-0.4995, p<0.0001) and with long-term mean SST (Mantel r=-0.5908, p<0.0001). Due to the strong effects of geographically persistent ocean currents in driving spatial patterns of ocean temperature, we used a partial Mantel test to examine the relationship between community similarity and ocean conditions while controlling for the effect of geographic distance. We found community similarity to be significantly correlated with long-term mean SST independent of geographic location (Partial Mantel r=-0.3656, p<0.0005). Furthermore, when removing the dominant environmental gradient (ocean temperature) from the geographic gradient, we found that distance among sites (while controlling for ocean temperature) was no longer correlated with community similarity (Partial Mantel r=-0.0347, p<0.3593).

DISCUSSION

The overall results of this study implicate temperature as a factor of great importance in

determining the composition of intertidal communities at the Channel Islands intertidal species. This finding is generally consistent with ideas developed by others working in this system over time (Hewatt 1946; Neushul et al. 1967; Murray and Littler 1981). Here we are able to quantitatively describe the correlations between species similarity and both geography and oceanography while accounting for spatial autocorrelation. The strength of the relationship between community similarity and SST was highly significant, even after accounting for the high degree of spatial autocorrelation in patterns of SST. Although a decay of community similarity with geographical distance may result from other, unmeasured environmental factors that are spatially autocorrelated (e.g., daylength, rainfall, etc.), long-term mean SST provides a reasonable index of oceanographic conditions known to influence benthic community structure (Broitman et al. 2005; Blanchette et al. 2006).

Despite the strong correlation between species similarity and spatially detrended ocean temperature, one must be cautious in interpretation of temperature, per se, as the driving factor in determining species distributions and community composition. In terms of oceanography, temperature is a useful proxy for the movement of water masses. Patterns of ocean circulation are complex here, and cold and warm water current systems collide in this region of the Channel Islands. Thus temperature as a proxy for oceanographic conditions can have important effects on the distribution of organisms through processes linked to larval and propagule dispersal. Temperature can also have direct effects on critical biological functions such as growth, survival and reproduction. Although the spatial patterns of species similarity described here are highly correlated with ocean temperature, we are unable to distinguish the processes underlying these patterns; however, this is a subject of future research in this system.

In addition to finding a strong link between species similarity and temperature, we also note a strong northwest to southeast pattern in similarity revealed in the pattern of site clustering (see Fig. 5). This spatial pattern seems to be largely driven by the relative abundance of particular functional groups across the island region. Blanchette et al. (2006) report similar findings at a smaller spatial scale across Santa Cruz Island. They found the abundance of sessile invertebrates to be greatest at the southeastern warm water sites, and macrophytes to be dominant at the colder water northwestern sites. Interestingly, we note a similar pattern across the larger island region. We found the abundances of sessile invertebrates (mainly barnacles and mussels) to be greatest at the warm water sites and the relative abundance of macrophytes to be highest at the cool water sites. This spatial pattern was also reflected in the abundance of mobile consumers, where herbivores (chitons, limpets, snails) tended to be more abundant at cool water sites, and carnivores (mainly whelks and seastars) were more abundant at warm water locations, suggesting that these bottom-up influences of temperature may propagate to higher trophic levels.

The identification of distinct benthic marine biogeographic regions has important implications for conservation, particularly to ensure that representative sites and their characteristic assemblages within regions are protected (Sink et al. 2005). This is particularly true for the Channel Islands, where marine reserves are becoming an important tool for conservation, and among many goals, are intended to protect the biodiversity and ecosystem functions as well as individually targeted species (Airame et al. 2003; McGinnis 2006). The

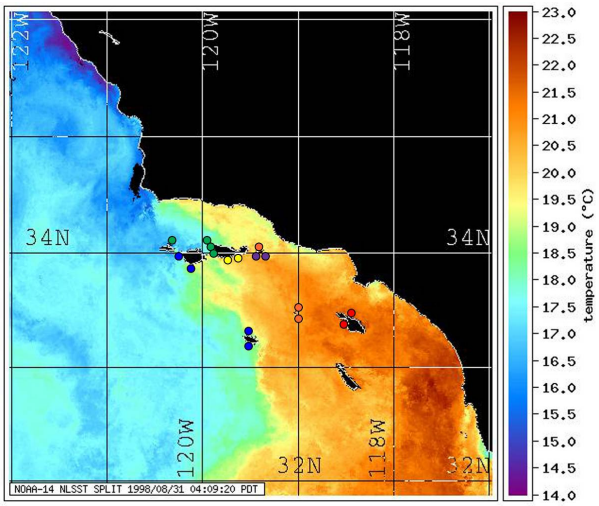

Figure 5. Colored dots overlaid on a regional image of Sea Surface Temperature (NOAA image from August 31, 1998) to illustrate the relationship between community similarity and oceanographic conditions. The dots are color coded to represent the site grouping colors used in Figure 4.

community-based approach to understanding biogeographic pattern is particularly relevant to conservation planning because regional differences in abundance of some taxa may reflect important ecological differences, such as contrasting trophic patterns that may indicate important ecosystem processes. The inclusion of different community assemblages in marine protected areas is likely to include the distinct smaller and or more rare taxa, which are usually not well sampled or studied. Furthermore, understanding the processes underlying spatial patterns of species similarity is also essential to forecasting the impacts of climate change. This study provides evidence that ocean conditions and likely temperature play a key role in the observed biogeographic patterns, and future changes in sea surface temperatures may alter the structure of these communities in unpredictable ways. Many climate change scenarios predict geographically patchy temperature changes (IPCC 2001; Helmuth et al. 2006) and may act to further divide biogeographic regions or alternatively to homogenize large regions. The knowledge gained from the present study of the distribution and abundance of intertidal species across the Channel Islands will help to provide a baseline against which the potential anthropogenic and natural changes of the future may be assessed.

CONCLUSIONS

Our findings reveal a high degree of spatial structure in the similarity of rocky intertidal communities of the Channel Islands, and are generally consistent with those of previously described biogeographic regions based on intertidal macrophytes. The strong correlations between similarity in community composition and both geographic position and SST suggest that both geography and oceanographic conditions act to drive spatial patterns. However, our results suggest that nearshore oceanographic conditions are the most important contributor to spatial patterns of species similarity across these islands.

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RECRUITMENT RESPONSE OF GUADALUPE CYPRESS (*CALLITROPSIS GUADALUPENSIS*) THREE YEARS AFTER GOAT ERADICATION ON GUADALUPE ISLAND

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Abstract—The only natural population of Guadalupe cypress (*Callitropsis guadalupensis*) occurs on Guadalupe Island, an oceanic island off the Baja California peninsula. This population has suffered an intense decline and a shift towards older individuals during the last 150 years, because feral goats have prevented recruitment of new individuals. After a goat eradication program began in 2004, intense seedling recruitment has been taking place in the Guadalupe cypress population. Our objective was to analyze how this new recruitment is occurring. We started in spring of 2004 with a demographic study of recruitment based on 515 new seedlings (< 1 year old) distributed inside forest patches and on patch borders. The new seedlings were labeled, and survival and growth were monitored each spring and autumn for three years. We also studied the spatial pattern of recruitment inside forest patches. We analyzed how gap size and percent canopy cover affected recruitment. Seed germination occurred both inside forest patches and along their borders, but mortality was higher in the forest interior than on the edge. Recruitment inside the forest was not clearly related to gap size or percent canopy cover. As a consequence, recruitment occurred mainly on the margins around the four patches, and more intensively in the west-southwestern borders.

INTRODUCTION

The Guadalupe cypress (*Callitropsis guadalupensis*, Cupresaceae) is, among the species of the genus *Callitropsis*, a paradigmatic case of geographical isolation and reduced population size. It is the only insular species of the genus, and its distribution is restricted to Guadalupe, a volcanic island located 260 km off the coast of Baja California, México (Fig. 1a).

Guadalupe is an oceanic island of about 250 km^2, characterized by a pronounced topography (highest point of 1295 m) and a climate controlled by frontal systems from the northwest, with an average annual precipitation about 133 mm (October to March) and monthly mean temperature varying from 16.2º C for April to 20.4º C for October (Moran 1996). However, there is a markedly climatic gradient from the higher northwestern part, with frequent fog and probably higher rainfall, to the more arid southern extreme of the island. Floristically, it is considered a geographic outlier of the California Floristic Province (Moran 1996).

The Guadalupe cypress is a tall tree (15–20 m) that presents a well defined trunk (mostly 30–60 cm thick) and a dense to rather open crown (Moran 1996). At present, the extant population forms a mono-specific forest of 148 ha with mean density of 110.7 individuals/ha, distributed among four forest patches (9, 47, 4, and 88 ha) at altitudes of 800–1300 m in the northwestern part of the island (Fig. 1b).

The introduction of goats on the island during the nineteenth century resulted in a process of environmental and biological deterioration (Moran 1996; León de la Luz et al. 2003) that dramatically affected the population dynamics of the Guadalupe cypress. It is difficult to know the extent of the original range, but information reported by the first naturalists who explored the island (e.g., Greene 1885; Bryant 1887; Franceschi 1893; Howell and Cade 1954) allows us to suppose a significantly more extensive cypress forest (Moran 1996; Oberbauer 2005). Although natural mortality and

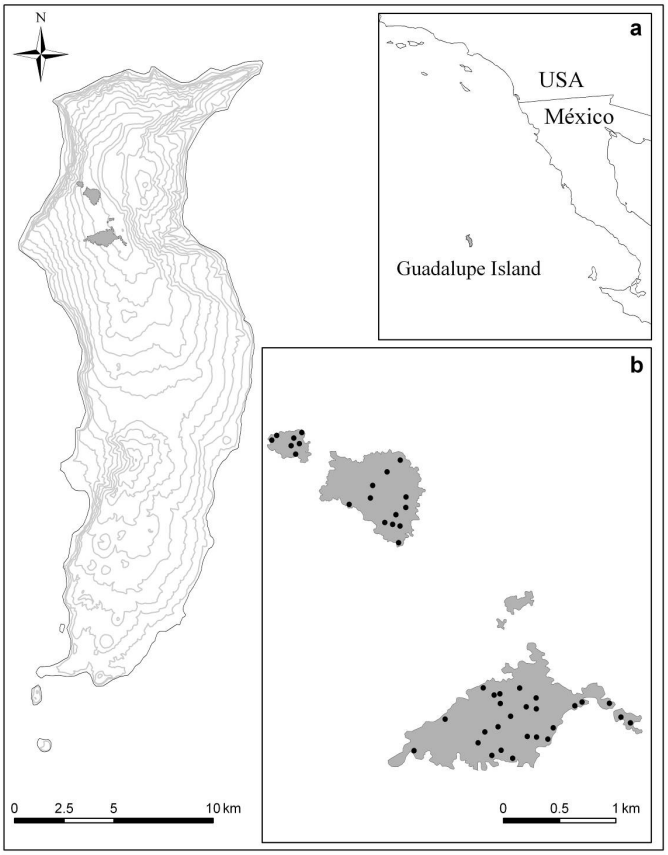

Figure 1. Guadalupe Island, showing (a) geographic location of Guadalupe Island; left panel: distribution of cypress patches (grey polygons) and contour lines at 100m intervals; and (b) locations of gaps analyzed inside the cypress patches.

occasional fires could have increased forest fragmentation (Moran 1996), the underlying cause of forest reduction has unquestionably been herbivory by goats, which prevents recruitment of new seedlings. The extinction risk caused by this situation compelled the Mexican government to declare this species as in "danger of extinction" (DOF 2001) and the IUCN to include it in its Red List under the category of "critical danger" (IUCN 2007).

After more than a century of island disturbance by goats, a multi-institutional program led by the Mexican governmental research agency Instituto Nacional de Ecología and the Mexican non-governmental conservation group Grupo de Ecología y Conservación de Islas started to eradicate the goats and restore the island in 2004. Two years later the goats were eradicated from Guadalupe Island.

As part of this program, a demographic study of the cypress population was started. The cypress patches on Guadalupe Island exhibit increased canopy gaps due to the high mortality of its aged population. Spatial canopy structure of the forest will affect seedling recruitment, because seedling establishment is a very sensitive stage in the life cycle of tree species (Harcome 1987), and it is well known that recruitment in other species of *Callitropsis* is a process positively affected by light availability (Vogl et al. 1977; Zedler 1981; Dunn 1987). Our hypothesis is that light availability also affects the recruitment process in *Callitropsis guadalupensis*. The objective of this work was to analyze how this heterogeneous scenario of light availability affected survival and spatial recruitment of cypress seedlings following goat eradication.

MATERIALS AND METHODS

Seedling Survival

We partitioned one of the large fragments (second northernmost patch in Fig. 1b) into three subjectively differentiated environments according to light availability on the ground. The first environment was "forest interior," which was defined as area away from edges of gaps and patches, and characterized by dense canopy and low light availability. The second environment was "forest edge," which was the area delimited by the vertical projection of the tree crowns located at the forest limit and characterized by medium light availability. The third environment was "forest exterior," which was defined by an exterior band of approximately 10 m from the limit of the previously defined edge, and characterized by absence of canopy and higher light availability. The 10 m width of this band was defined by the distance of the most remote seedling found.

We searched all three environments for cypress seedlings in May and October 2004, and we measured and labeled all seedlings we found. We labeled a total of 515 cypress seedlings (Table 1). Of the 383 seedlings found in May, 90 were located in the interior, and 293 were on the edge. In October, 4 seedlings were found in the interior, 42 were found in the edge, and 86 were found in the exterior. Height and crown diameter of all individuals were measured, and seedlings were grouped into three size categories: small (S1; height $\leq$ 1 cm), medium (S2; 1–4 cm), and large (S3; height > 4 cm). Size classification was selected in order to have height categories useful in the three environments. These categories also reflected the population structure observed in the field. From May 2004 to October 2006, we recorded survival of the labeled individuals twice each year—once at the end of the rainy season (May) and again at the end of dry season (October). In each survey period, we recorded the condition of the plant (dead or alive) and its height.

Table 1. Abundance and size structure of the labeled cypress seedlings among the three environments. Plant size categories: S1 $\leq$ 1cm, S2 = 1–4 cm, and S3 > 4 cm. Forest environments: interior, edge, and exterior of forest patch.

	S1	S2	S3
Interior	63	31	0
Edge	32	220	83
Exterior	0	30	56

Survival functions are a common statistical tool for characterizing and summarizing the risk of dying in a population. If such an analysis is to be performed, there are two main aspects that must be taken into account. The first is related to the fact that survivorship can change through time (Deevey 1947). It is therefore important to include the temporal variation of the risk of dying in the modeling of survival process. The second involves the type of data used to fit the survival model. Due to biological and methodological restrictions, sometimes it is not possible to quantify the complete span of life of an individual. That is, there are individuals in the population that have no date of death (they outlive the observation period, or migrate, or simply disappear). Such subjects may yield information about surviving, but not for dying (Crawley 1993). A function widely used for modeling survival processes is the Weibull function (Weibull 1951). One of its main advantages is that it can model several shapes of curves (Ebert 1999), allowing the data to determine whether the risk of dying is constant or not. Also, it is possible to include in the analysis those individuals we know that die and those about whom we have no certainty.

Survivorship—the probability that seedlings survive to time t—is described by the Weibull survival function: $S(t) = e^{-(\alpha \cdot t^{\gamma \cdot \mu})}$ where $S(t)$ represents the proportion of seedlings that survive to time t, and α, γ, and μ are scale, shape, and treatment parameters, respectively. The value of α indicates how the hazard of death changes with time. If $\alpha = 1$, the hazard is constant; if $\alpha > 1$, then the hazard increases with age; and finally, if $\alpha < 1$, it decreases with age (Crawley 1993). To estimate the parameters α, γ, and μ, we fit the Weibull model to survivorship and time data using the statistical software "R" (R Development Core Team 2007). Some data were considered as "right censored" (some individuals survived the experiment and were used to estimate the survival function, but not the function of mortality) and some were considered as "interval" type (some individuals were added to the experiment after it started). The survival package of R was used to take into account these aspects (Therneau and Lumley 2007).

The independent variables used in this regression model include one continuous (time to death) and two categorical (seedling size and environment) with three levels each. Therefore, we obtained the average effect of treatment, standard errors and the significance level for all the regression parameters in each analysis. Since the three size categories of seedlings are not present in all the environments (Table 1), we performed independent analyses for each environment. Survival of small (S1) plants was compared between the "forest interior" and the "forest edge"; survival of medium (S2) plants was compared in all the environments; and survival of large (S3) plants was compared between the "forest edge" and the "forest exterior."

Seedling Recruitment

In November of 2006, we randomly selected 44 canopy gaps in the forest patches (Fig. 1b), and for each one we measured gap size, percent canopy, and number of seedlings. We measured the distance from the center of each gap to the trunk of the nearest tree. We used this distance as the radius of the gap circle and then calculated the gap size as the area of this circle. In ArcGIS, we added a concentric buffer of 15 m (approximate average individual crown diameter) around each gap circle to create the buffered gap circle (gap radius + 15 m). We used ArcGIS to calculate the canopy area found inside the buffered gap circle. We defined the percent canopy as the proportion of canopy area with respect to the area of the buffered gap circle. Association between seedling number and two gap locations (near the edge vs. interior of forest) was tested with a χ^2 test. To examine the relationship between seedling recruitment and gap characteristics, we employed the linear regression models $D=\beta_1 A - \beta_2$ and $D=\beta_3 C - \beta_4$ to determine how density of seedlings (D) is influenced by gap size (A) and percent canopy (C), respectively.

RESULTS

Seedling Survival

We found a significant effect of light environment on survival of different size cypress seedlings. Survival of small plants was significantly higher at the edge than inside the forest ($P <$ 0.0001). All the small seedlings (S1) in the interior of forest were dead at the end of census, whereas at the edge 20% of small seedlings survived (Fig. 2a). Medium seedlings (S2) showed similar behavior, with significantly higher mortality in the interior of the forest than at the edge ($P = 0.01$) or at the exterior of the patch ($P < 0.0001$) (Fig. 2b, Table 2). Finally, survival rate of large seedlings (S3), which was the highest rate of the three sizes and greater than 90%, was not significantly different between the edge and the exterior of the forest (Fig. 2c, Table 2).

The shapes of the survival curves are different for each environment (Fig. 2). In the interior of the forest the curves show high mortality in the initial stages. However, in the environments with more light, mortality is higher in the final stages. In

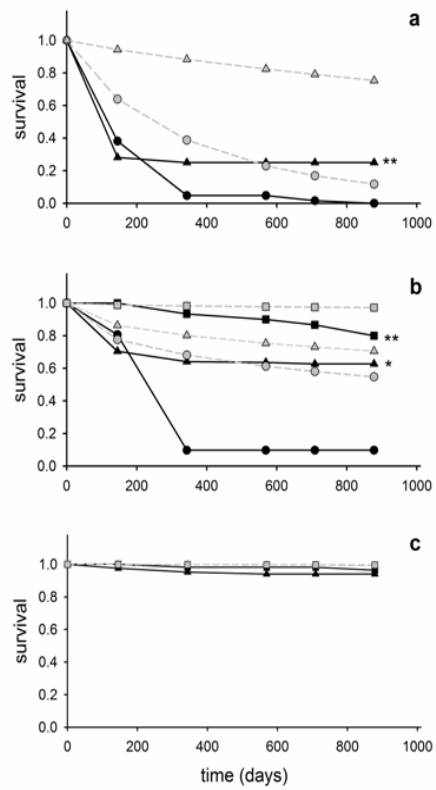

Figure 2. Survival curves of cypress seedlings according to environment and height category. (a) small plants (height = 1 cm); (b) medium plants (h = 1–4 cm); and (c) large plants (h > 4 cm). Solid black lines indicate observed survival, and dashed gray lines indicate estimated survival. Forest interior is denoted by circles, edge by triangles, and exterior by squares. Asterisks refers to survival curves significantly higher than the interior survival curve (*P = 0.01; **P < 0001).

Table 2. Coefficients of Weibull survival curves and their significance levels, compared against the first level of the factor. Plant size categories: S1 < 1cm, S2 = 1–4 cm, and S3 > 4 cm. Forest environments: interior, edge, and exterior of forest patch.

	γ	α	μ	s.e.	z	P
S1						
Interior	0.869	1.000	0	0.145	0	
Edge	0.869	0.131	2.33	0.313	7.43	< 0.0001
S2						
Interior	0.480	0.395	1.93	0.399	4.84	
Edge	0.480	0.228	3.07	0.472	2.42	0.0157
Exterior	0.480	0.018	8.32	0.973	6.56	< 0.0001
S3						
Edge	0.793	0.003	7.11	0.843	8.442	
Exterior	0.793	0.002	7.80	0.776	0.884	0.3770

general, the values in the regressions are < 1, which suggests that the risk of dying diminishes with age (Table 2). The only exception was the curve of the S1 plants in the interior of the forest, where value was equal to one, indicating that the risk of dying is constant over time.

Seedling Recruitment

The gaps ranged in size from 127 m^2 to 2827 m^2 (average value of 1175 m^2), and we found values of seedling density from 0 to 0.091 seedlings/m^2, with an average density of 0.013 seedlings/m^2. The linear regression indicated a higher density of seedlings in gaps with a larger gap area ($\beta_1 = 0.018$, $\beta_2 = 3.43$, $R^2 = 0.1631$, $P = 0.0038$) and at sites with a higher percent canopy ($\beta_3 = 0.023$, $\beta_4 = 38.62$, $R^2 = 0.1668$, $P = 0.0034$). Results of the χ^2 test also indicated that there was higher seedling density in gaps within 50 m of the forest edge than in interior gaps. All 18 gaps close to the edge had seedlings, whereas only 10 of the 26 gaps in the interior of the forest were occupied ($\chi^2 = 19.18$, $df = 1$, $P < 0.0001$). Seedling density in the border gaps (0.028 ± 0.026 *s.d.* seedlings/m^2) was four times higher than in the interior gaps (0.006 ± 0.006 *s.d.* seedlings/ m^2) ($t = 3.38$, $df = 20$, $P = 0.003$).

DISCUSSION

Cypress vital rates seem to be significantly related to the type of environment and size class. The interior of the forest appears to be the most restrictive environment. We did not find large seedlings (S3) inside the forest, and survival rates of the two other size classes found (S1 and S2) were almost zero after the first year. In contrast, survival at the edge and exterior of the forest were significantly higher. It is very likely that the main abiotic factor involved is light availability. This strong light requirement is reported in other studies of cypress species (Vogl et al. 1977; de Gouvenain and Ansary 2006). However, seedling recruitment inside the forest showed a strong relationship with edge proximity, in addition to gap size or percent canopy cover around the gap. Due to the fact that some factors can be correlated in a gap (e.g., light, temperature, and humidity), it is possible that other environmental factors besides light may be affecting seedling recruitment, such as water availability caused by fog influence (Garcillán, personal observation) Biological processes may also be important, like higher seed production at the edge, or higher concentration of seeds in the soil downslope of the western borders, due to water transport after rain. All these factors deserve to be experimentally tested in order to gain understanding of the seedling recruitment. In this context, it is possible that this remnant population, even with its high disturbance level, can exhibit "classical" gap dynamics like that of tropical and temperate forests (Pickett and White 1985; Barnes et al. 1998).

Seedling survival increases with size. Small plants suffered elevated mortality in any light environment, whereas medium size seedlings showed higher survival, even in the interior. Survival of plants taller than 4 cm is almost 100% in the edge and the exterior of forest. These findings coincide with previous studies of other species (e.g., Turner 1990; Masaki and Nakashizuka 2002). This study suggests that the seedling height of 4 cm may be considered as a survival threshold; above which mortality is very low. The existence of such a threshold, although of higher value, is reported for other tree species (Harcombe 1987). This pattern is perhaps evidence that these species face similar pressures at the initial growth stages. They must reach a size that allows them to tolerate shadowing, dryness, competition, pathogens, and other selection pressures. Nevertheless, more studies are needed in order to confirm this finding. In a similar way, values show that survival also increases with age (Streng et al. 1989; Sacchi and Price 1992). However, some caution must be taken with this conclusion, because age is not always a fine indicator of seedling strength. Finally, there may be some other processes influencing seedling survival that cause an overestimation of the predicted survivorship curves. In order to have a better fit, other factors like soil properties may be added to improve the model.

This study provides information for the development of a management and recovery program for this species. The ongoing natural recruitment process can be accelerated through collecting seeds and sowing them in strategic zones, like gaps near the edge of the forest. Also, natural recruitment can be supplemented with the introduction of new individuals grown in greenhouses. Trees have several ecological roles (Jones et al. 1997), so it is very likely that some key ecosystemic processes of the island (like water infiltration to the ground) will be increased if the forest cover grows up.

Fortunately, the extinction risk of the Guadalupe cypress has diminished considerably, owing to the first recruitment of seedlings after perhaps more than a century. Nevertheless, the demographic viability of this species depends on the development of a robust population structure that will allow it to face the evolutionary processes (inbreeding or genetic drive) and hazards (e.g., pathogens, fires) that may extinguish a small isolated population. Although many years are needed before such a population structure can be achieved, the observation of new individuals, less than 3 years old, which are already producing reproductive cones, suggests a very promising future for this species. These good signs reflect the efforts of many persons, institutions, and organizations to stop ecosystem degradation and recover the biological richness of Guadalupe Island.

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RESTORATION STRATEGIES FOR OVERCOMING LIMITATIONS TO SCRUB OAK REGENERATION ON CATALINA ISLAND

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Abstract—When the removal of feral pigs and goats from Catalina Island by 2002 did not produce a flush of island scrub oak seedlings, and observations of patches of dying mature oaks increased, a study was initiated to identify possible limiting factors to scrub oak regeneration. The study addressed two current potential island-wide factors: herbivory by non-native deer and bison, and competition from non-native annuals, primarily grasses. Also addressed were soil-mediated differences among potential restoration sites (eroded slopes, oak-dieback areas, and healthy oak stands), microsite characteristics related to proximity to oak canopy, and the potential value of tree-tubes to oak seedling growth and survival. After three years, data indicate that microsite characteristics related to seedling proximity to oak canopy cover and the use of tree-tubes have more significant impacts on growth and survivorship than protection from ungulate herbivory with fences, annual grass control, or soil-mediated site differences. Soil nutrients, moisture, and texture as well as pathogen loads were monitored but their impacts on oak seedlings were not consistent.

INTRODUCTION

On Catalina Island, the lack of saplings and limited number of seedlings of island scrub oak (*Quercus pacifica*) have been attributed to non-native ungulates. During the last two centuries, bison (*Bison bison*), pigs (*Sus scrofa*), goats (*Capra hircus*), and deer (*Odocoileus hemionus*) were introduced to the island. They proliferated, contributing to acorn, seedling, and basal sprout herbivory (Griffin 1971; Peart et al. 1994; Sweitzer and Van Vuren 2002; Manuwal and Sweitzer 2006). By 2002, 99% of the feral pigs and 100% of the goats were removed from Santa Catalina Island (Schuyler et al. 2002a, b). However, oak regeneration did not increase as dramatically as expected, and, at the same time, patches of dying mature oaks (hereafter referred to as "dieback" areas) were noted on the channel side of the island. A more recent examination of historical aerial photographs suggests that patches of scrub oaks have been slowly dying over the past 80 years with no indication of regeneration (Knapp, in press).

Dieback may be attributed to site-specific characteristics that may have decreased the vigor of trees and made them vulnerable to soil-borne pathogens. However, it may also be indicative of forest senescence, since the lack of regeneration coincides with high rates of goat and pig herbivory on the island, leaving only mature trees. Senescence is a greater concern for the long-term persistence of oak woodland than localized "dieback" because it suggests a much wider-scale loss of mature, acorn-bearing oaks. Without identifying and mitigating the limiting factors to natural scrub oak regeneration, Catalina Island stands to lose the scrub oak woodland ecosystem that covers 33% of the island. The observed lack of seedling regeneration and dieback raises concern that a permanent habitat transformation from oak woodland to annual grassland could occur, leading to the establishment of a less diverse and non-native dominated alternative stable state (George et al. 1992; Suding et al. 2004; Acacio et al. 2007).

The numerous studies in California on limitations to oak regeneration implicate multiple factors. Oaks do not form a persistent seed bank, and regeneration has been shown to be limited by herbivory of acorns and seedlings (Menke and Fry 1980; Adams et al. 1992; Groot Bruinderrink and Hazebrock 1996). Although pigs and goats have been removed from Catalina Island, deer and bison remain and continue to be a potential threat to young oaks. Acorn predation by rodents, such as ground squirrels (*Spermophilus beecheyi nesioticus*) or mice (*Peromyscus maniculatus catalinae*), may also

contribute to reduced regeneration (Linsdale 1946). Competition from established annual grasses is a second factor thought to limit oak regeneration. Studies have implicated non-native annual grasses such as *Bromus diandrus*, common on Catalina Island, as one of the primary factors responsible for reducing soil moisture (Knoop and Walker 1985; Zutter et al. 1986; Gordon and Rice 2000), and inadequate soil moisture has been shown to limit regeneration of oaks (Gordon and Rice 1993; Swiecki et al. 1997; Gordon and Rice 2000; Davis et al. 1991). Finally, oak regeneration and growth may be sensitive to soil characteristics that vary among potential restoration sites, as well as microsite conditions that are related to proximity of the parent canopy (Tyler et al. 2002). Potential restoration sites include large gaps in scrub oak woodlands caused by localized dieback or by loss of tree cover and erosion due to past impacts of feral ungulates. In these patch types, soil-mediated characteristics such as reduced water-holding capacity (e.g., sandy, eroded soils) or soil pathogens (e.g., dieback areas) are potential limiting factors. Studies have also shown that partial shade increases survivorship of another drought tolerant oak species, *Quercus douglasii* (Callaway 1992), because of reduced water stress (Muick and Bartolome 1987). Furthermore, proximity to conspecific parents may allow beneficial mycorrhizal symbionts to colonize seedlings more readily and facilitate nutrient uptake (Dickie et al. 2002). Therefore, seedlings growing under the canopy edge might experience benefits from ready mycorrhizal colonization, relief from evaporative demand provided by the partial shade, and fog drip from the canopy drip line, while seedlings in the open may benefit from full sun and reduced competition from mature trees and impacts from associated soil pathogens.

This study compared the effects of herbivory, competition from annual grasses, oak canopy shade, and soil condition as potential factors limiting scrub oak regeneration. Additionally, I evaluated the effectiveness of two methods (tree-tubes vs. fences) for limiting ungulate impacts, and examined the influence of different restoration patch types (eroded, dieback, and healthy) on oak recruitment. This design allows us to identify key limiting factors to island scrub oak regeneration, while concurrently evaluating the success of potential restoration strategies needed to mitigate these factors.

MATERIALS AND METHODS

A field experiment was conducted on Catalina Island to evaluate the success of various restoration strategies for reducing the impacts of potential limiting factors to scrub oak regeneration. Using a series of factorial designs, I evaluated herbivory with fencing and tree tubes; considered competition with annual grasses using herbicide treatments; considered microsite characteristics by planting in canopy and open field sites; and evaluated the impact of erosion and dieback on soils by planting in three different sorts of patch types: eroded, dieback, and healthy oak stands.

Herbivory

Herbivory was examined using fencing treatments in a factorial study with competition and microsite factors within healthy oak stands ("H" in Table 1). Within patches of healthy oak woodland, groups of planted acorns were exposed to combinations of three herbivory treatments (fenced, tree-tube, control), two competition treatments (weeded, unweeded), and two microsite treatments (open, edge). In each patch, 40 sites were planted for each of the 12 groups representing treatment combinations. This was replicated over five patches. However, one patch burned in a wildfire in 2007, and we only analyzed data for the remaining four patches.

The impacts of herbivory and possible ways to circumvent it were evaluated with three treatments: fencing, tree-tubes, and a control. Within each healthy patch, there were four treatment combinations (competition and microsite) each with 40 acorn planting sites for a total of 160 acorn planting locations ("sites") assigned to each herbivory treatment. Those in the "fenced" treatment were enclosed within a single fenced area that included trees and sufficient open space to accommodate the microsite and competition treatment combinations. The 2.4 m tall plastic deer fence was supported by 3 m t-stakes with a top wire. A large fenced area was used rather than many individual fences to simulate the wide-scale loss of herbivory and potential for increased grass cover and associated reduced soil moisture that may result if deer and bison are removed from the island. Outside the fenced area, acorns in the 160 "tree-tube" treatment sites, from the four microsite x

Table 1. Study design. (H) indicates treatment combinations used to examine effects of herbivory. (C/M) indicates treatment combinations used to examine effects of competition and microsite. (PT) indicates treatment combinations used to examine patch type. Within each patch replicate, there are 40 planting sites per treatment combination.

		HEALTHY (n = 4)		DIEBACK (n = 5)		ERODED (n = 5)	
		Edge	Open	Edge	Open	Edge	Open
FENCED	Weeded	H,C/M	H,C/M	C/M	C/M		
	Unweeded	H,C/M	H,C/M,PT	C/M	C/M,PT		PT
TREE-TUBES	Weeded	H,C/M	H,C/M	C/M	C/M		
	Unweeded	H,C/M	H,C/M,PT	C/M	C/M,PT		PT
CONTROL	Weeded	H	H				
	Unweeded	H	H				

competition treatment combinations, were planted in tree-tubes (Tubex™, Treessentials, St. Paul, MN). In the event that large herbivores cannot be removed from the island, tree-tubes have been shown to have success in previous oak restoration projects (Stratton 2005), and may be a feasible strategy for reducing herbivory on oaks. Tree-tubes have been shown to have minimal effect on solar insolation on oaks because of low photosynthetic rates, and to improve growing conditions by moderating the temperature and increasing CO_2 (Frearson and Weiss 1987). Tree-tubes may also protect planted acorns from rodent predation. In addition to fenced and tree-tube treatments, acorns were planted in 160 control sites that were located outside the fenced area, without the use of tree-tubes.

Competition and Microsite

To address the effects of weed competition, sites assigned to "weeded" treatments were treated with annual spring applications of herbicide (Round-up Pro™, St. Louis, MO) to kill grass and forbs within a 1-m diameter circle around the seedlings. McCreary and Tecklin (1997) demonstrated that this is an effective weed control technique for oaks. Herbicide was applied in 2005 and 2006, but not 2007 due to the low rainfall (79 mm versus 345 mm long-term average, unpublished data) and the early death of annual grasses. No herbicide was applied to "unweeded" sites.

Microsite characteristics related to proximity to the oak canopy were evaluated by locating planting sites either along the canopy edge ("edge") along the dripline or in open areas at least 2 m from tree canopies ("open").

To examine the effects of weed competition (C) and microsite (M) on oak regeneration, two weeding treatments (weeded, unweeded) and two microsite treatments (open, edge) were evaluated over two restoration patch types (healthy, dieback) and two herbivory treatments (fenced, tree-tubes; see "C/M" in Table 1). Competition and microsite were not evaluated in the eroded patch type, because these patches lacked both ground vegetation and canopy cover. The eight treatment combinations were replicated in four healthy patches and five dieback patches. Within each patch, 40 planting sites were assigned to each treatment combination. Soil moisture was monitored gravimetrically from the four fenced treatment combinations (2 weeding treatments x 2 microsite treatments) in each of the five healthy and five dieback patches at the end of the dry season in 2006. Volumetric soil moisture was also monitored with capacitance-type sensors that measure the dielectric constant or permittivity of soil (Decagon ECH20 Sensors, Pullman, WA) hourly from May 2005 though January 2006 with three replicate 4-sensor arrays in fenced healthy plots to compare microsite and competition factors.

Restoration Patch Types

The effect of planting sites on oak recruitment from acorns was examined by evaluating three potential restoration patch types: stands of healthy oaks (healthy patches), areas experiencing the unexplained dieback of mature oaks (dieback patches), and bare, eroded sites within oak groves where we might want to re-establish oaks to restore

soil stability and continuity of the oak woodland (eroded patches). Five patches were selected to represent each restoration patch type. All 15 patches were located on the channel side of Catalina Island on northwest-facing slopes of less than 20% grade between Toyon Bay and Empire Landing. Three weather stations placed across the range of sites and a year of data showed no difference in environmental factors (Stratton, unpublished data). Soils ranged from dense sandy clay soils in the eroded sites to loamy, organic soils within oak stands. To characterize the soils for texture and nutrient values, composite soil collections were made from 0–10 and 10–20 cm depths from five replicates of each of the three patch types in edge and open positions (only "open" was sampled in the eroded patches). Soil texture and nutrients were quantified for each sample at San Diego State University Soils Lab. There were no differences by depth so the two depths were pooled when calculating the mean for each patch type.

Within each patch type, fenced and tree-tube treatments compared the relative success of these two techniques for limiting herbivory. Because eroded patches lacked both ground cover and oak canopy, interactions with weed competition or microsite could not be evaluated among all patch types. Therefore, all planting sites were located in open areas, and acorns in eroded patches were not subjected to a weeded treatment. In healthy and dieback patches, the open grown unweeded treatments were used for the comparison with the open grown seedlings from the eroded patch type (see "PT" in Table 1). In all replicates of the three patch types there were 40 planting sites associated with each open-planted, herbivory treatment (fencing, tree-tubes).

Planting and Data Collection

More than 35,000 acorns, without insect holes and moist enough to sink in water, were collected in fall 2004 from 68 sites between Bulrush Canyon and Empire Landing. All acorns were stored in flats in moist sand and peat in a cold storage facility for two months and then sorted evenly such that each treatment combination had a stratified mix of 320 acorns representing all collection sources. Eight acorns were planted in each of the 40 acorn planting sites per treatment combination, to ensure that initial germination results would not greatly limit the replication in the study design. All planting was conducted during the first week of December 2004 after a significant rainfall event. All planting locations were > 2 m apart, marked with painted rebar, and identified by unique numbers on metal tags.

In 2005, germination rate for each treatment was calculated as the percentage of planted acorns that germinated. Afterward, all but the tallest seedling in each location were clipped, leaving one seedling per site. Between 2005 and 2007, the growth (height) and survivorship of seedlings were monitored annually in June. In 2007, vigor was assessed for each seedling, and evidence of herbivore or insect damage was noted. High vigor seedlings had new growth and little damage, while low vigor seedlings were significantly dessicated and had lost leaves. The majority were rated intermediate so only the high and low vigor are reported here because they were in notably healthier or poorer condition. Within each patch, survivorship was calculated for each treatment combination as the percentage of the 40 sites whose seedlings had survived. Likewise, percent high/low vigor and percent herbivore/insect damage were calculated from the 40 sites per treatment combination within each patch.

Data Analysis

As aforementioned, one healthy patch burned in 2007, so data from this patch were not used in any of the seedling analyses. A three-way ANOVA (Minitab, Minitab Inc., State College, PA) was used to analyze data within the remaining four healthy patches. To assess the importance of herbivory, I compared the three levels of the herbivory treatment (fenced, tree-tube, control), using microsite location and weeding treatment as covariates. Each level of the fencing treatment was replicated at the level of each treatment combination group. Analyses were performed for the response variables germination, survivorship, height, percent low vigor seedlings, percent high vigor seedlings, percent herbivore damage, and percent insect damage. Because analyses were already sufficiently complex and because treatments such as herbicide were not equivalent among years, survivorship and height data for each year (2005–2007) were analyzed separately. Post-hoc two-sample t-tests followed by False Discovery Rate (FDR) analyses were

performed where there were three factors in order to compare each pair separately and consider multiple comparisons.

To look at effects of competition and microsite on oak regeneration, I analyzed data from two levels of the weeding treatment (weeded, unweeded), two levels of the microsite treatment (canopy edge, open field), and used fencing treatment (fenced, tree-tubes) and two levels of patch type (healthy, dieback) as covariates. A general linear model was required rather than ANOVA, because the number of replicates was uneven among patch types. Response variables analyzed were germination, survivorship, height, percent low vigor, percent high vigor, percent herbivore damage, and percent insect damage. Where there were three factors, post-hoc two-sample t-tests followed by FDR analyses were performed. The general linear model was also used to compare mean gravimetric soil moisture readings between the weeded and unweeded, and edge and open groups within fenced treatments of healthy and dieback patches. A general linear model was also used to compare daily volumetric soil moisture averages over 187 days from three replicate 4-sensor arrays (competition and microsite treatment combinations) in healthy plots using array location as a factor in order to capture the power of the mean daily soil moisture averaged from hourly samples.

To evaluate the success of potential restoration strategies, I used a general linear model to compare oak regeneration in open, unweeded sites across three potential restoration patch types (healthy, dieback, eroded) and two herbivory treatments (fenced, tree-tube). In healthy and dieback patches, the data from unweeded open site treatments were compared with the eroded patches which were all open and unweeded. Response variables analyzed were germination, survivorship, height, percent low vigor, percent high vigor, percent herbivore damage, and percent insect damage. As with the other analyses, post-hoc two-sample t-tests followed by FDR analyses were performed where there were three factors.

RESULTS

Rainfall was significantly above the long-term average of 345 mm during 2005 (759 mm) when the acorns were germinating, but was below average in the ensuing two years of the study (269 mm and 79 mm). Tyler et al. (2002) found that acorn germination rates and initial survivorship are highly correlated with rainfall. Average acorn germination rates were 27%; however, because 8 acorns were planted at each of the 40 planting locations per treatment combination, the effective seedling establishment rate for the study averaged 80%.

Herbivory

Table 2 summarizes the results of ANOVA within healthy patches. In this table, interaction terms are not presented unless significant. Germination rates did not differ among the herbivory treatments, fenced ($\bar{x}$ = 28.3), tree-tube ($\bar{x}$ = 26.1), and control ($\bar{x}$ = 27.2) (Table 2). Survivorship among herbivory treatments was not significantly different in the first two years (Table 2; Fig. 1). However, by the third year the tree-tube-protected seedlings (49%) began to survive at a significantly higher rate than seedlings in the fenced (28%; $p = 0.042$) or control sites (22%; $p = 0.0025$). Seedling growth (height) was significantly different among herbivory treatments in 2006 and 2007 (Table 2), with post-hoc tests indicating that mean heights of tree-tube protected seedlings were taller than those of fenced seedlings, which were taller than control ($p < 0.05$ for all comparisons; Fig. 1). The fenced and control groups had a very low mean percentage of seedlings rated high vigor (1% and 2% respectively), while on average, 11% of tree-tube groups had seedlings that were classified as high vigor (Tables 2, 3). Fenced and control groups also had a higher proportion of seedlings rated "low vigor" compared to those protected by tree-tubes, but these differences were not significant (Tables 2, 3). A higher percentage of the seedling damage in fenced and tree-tube treatments was attributed to insects rather than herbivores ($p < 5\%$; Table 3). There were no significant interaction effects within this analysis.

Annual Grass Competition

Table 4 summarizes the results of the general linear model analysis within healthy and dieback patches. The mean volumetric soil moisture percentage in weeded planting sites (11.5%) was significantly higher than unweeded sites (9.9%; Table 4). Acorn germination was higher in weeded

Table 2. ANOVA tests of effects for treatments within healthy patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
Germination	2005	Herbivory	2	45.5	22.7	0.17	0.847
		Competition	1	544	544	3.99	0.51
		Microsite	1	2305	2305	17.02	0.000
Survivorship	2005	Herbivory	2	28.4	14.2	0.03	0.967
		Competition	1	516.8	516.8	1.23	0.274
		Microsite	1	3631.4	3631.4	8.62	0.005
	2006	Herbivory	2	587.8	293.9	0.73	0.486
		Competition	1	1813	1813	4.53	0.039
		Microsite	1	12192	12192	30.47	0.000
	2007	Herbivory	2	6309	3154	12.15	0.000
		Competition	1	1752	1752	6.75	0.013
		Microsite	1	10208	10208	39.32	0.000
Height	2005	Herbivory	2	1.1147	0.5573	4.42	0.018
		Competition	1	0.4565	0.4565	3.62	0.064
		Microsite	1	0.1706	0.1706	1.35	0.251
	2006	Herbivory	2	8.6517	4.3259	13.79	0.000
		Competition	1	0.868	0.868	0.28	0.602
		Microsite	1	0.1382	0.1382	0.44	0.510
	2007	Herbivory	2	13.019	6.509	15.99	0.000
		Competition	1	0.1005	0.1005	0.25	0.622
		Microsite	1	0.0495	0.0495	0.12	0.729
%Low vigor	2007	Herbivory	2	24547	12274	2.63	0.084
		Competition	1	4750	4750	1.02	0.319
		Microsite	1	10730	10730	2.30	0.137
%High vigor	2007	Herbivory	2	934	467	9.40	0.000
		Competition	1	72.81	72.81	1.47	0.233
		Microsite	1	51.35	51.35	1.0	0.315
%Herbivore damage	2007	Herbivory	2	854	427	2.75	0.075
		Competition	1	74.2	74.2	0.48	0.493
		Microsite	1	440	440	2.84	0.099
%Insect damage	2007	Herbivory	2	5803	2901	5.05	0.011
		Competition	1	276	276	0.48	0.492
		Microsite	1	144	144	0.25	0.619

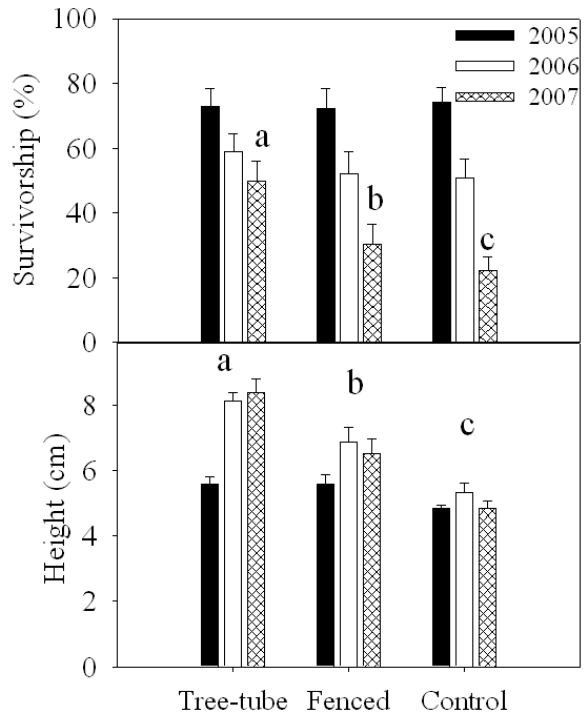

Figure 1. Mean survival and height of seedlings among three herbivory treatments within healthy patches for three years of study (n = 16 for each treatment). Letters (a,b,c) indicate treatments that are significantly different from each other at α =.05, as determined by post-hoc 2 sample t-tests.

plots ($\bar{x}$ = 31%) than unweeded plots ($\bar{x}$ = 24%) in both patch types and across fencing and microsite treatments (p = 0.0001; Table 4). For all years, seedlings in the weeded treatment had higher total survivorship than seedlings in the unweeded treatment (Table 4; Fig. 2). Weeded seedlings, however, were not significantly taller than unweeded seedlings (Table 4; Fig. 2). Weeded treatments had a significantly higher proportion of high vigor seedlings (Table 3); however, the weeding treatment had less effect on height or survivorship than other treatment comparisons.

Microsite

Within healthy and dieback patches in the fenced and tree-tube treatments, microsite characteristics related to canopy cover showed the largest effect on oak regeneration. Beginning with higher mean acorn germination in open sites ($\bar{x}$ = 35%) compared to canopy edge ($\bar{x}$ = 21%; Table 4), open field seedlings had higher survivorship across all patch types and herbivory (fencing type) treatments (Table 4; Fig. 3). The survivorship pattern is consistent across all three herbivory treatments: tree-tube seedlings had significantly higher survivorship overall and double the survivorship out in the open (63%) compared to in the canopy edge (31%). Fenced seedling survivorship, while lower overall, was also nearly three times higher in the open (38%) than in the canopy edge (13%). Within the healthy patches, seedlings in control treatments that were grown in the open had 31% survival compared to canopy edge at 12%. Seedlings in open treatments only showed slightly higher growth than seedlings in edge treatments (Table 4; Fig. 3) While soil nutrients were higher under the canopy edge (Table 5), soil moisture was slightly lower (8.5%) compared to 11% for open sites (Table 4).

Table 3. Vigor and damage assessments by treatment comparisons. Data reflect mean percentages of surviving seedlings/replicate in 2007 rated as high or low vigor; as damaged by herbivores (deer and bison combined) or insects. Significant differences to the p<0.05 level are noted with a/b notation, as determined by post-hoc t-tests. Means represent values only from those treatments common to the factors evaluated in each set of rows (divided by lines).

Treatment (n)	% High vigor	% Low vigor	% with herbivore damage	% with insect damage
Healthy (8)	4.6	28.2	0.62	70.2
Dieback (10)	19.3	22.5	5.89	56.9
Eroded (10)	19.6	32.5	0.18	62.1
Fenced (16)	1.5 a	82.9	5.2	79.9
Control (16)	2.4 a	50.1	11.6	54.5
Tree-tubes (16)	11.3 b	27.8	1.4	75.0
Weeded (36)	15.9 a	47.0	4.2	73.9
Unweeded (36)	7.8 b	31.9	5.5	66.4
Open (36)	17.9 a	27.9	3.8	66.2
Canopy edge (36)	5.8 b	51.0	5.9	74.0

Table 4 . General Linear Model tests of effects for treatments common to healthy and dieback patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
Germination	2005	Competition	1	998.7	998.7	12.32	0.001
		Microsite	1	4128	4128	50.93	0.000
		Herbivory	1	26.2	26.2	0.32	0.572
		Patch Type	1	44.3	44.3	0.55	0.462
Survivorship	2005	Competition	1	1088	1088	4.07	0.048
		Microsite	1	7708	7708	28.84	0.000
		Herbivory	1	58.7	58.7	0.22	0.641
		Patch Type	1	636.7	636.7	2.38	0.127
	2006	Competition	1	3368.8	3368.8	9.53	0.003
		Microsite	1	16577	16577	46.87	0.000
		Herbivory	1	4958	4958	14.02	0.000
		Patch Type	1	844.1	844.1	2.39	0.127
	2007	Competition	1	1927.2	1927.2	6.58	0.013
		Microsite	1	17189	17189	58.67	0.000
		Herbivory	1	10332	10332	35.26	0.000
		Patch Type	1	243	243	0.83	0.365
Height	2005	Competition	1	0.119	0.119	0.26	0.615
		Microsite	1	0.003	0.003	0.01	0.932
		Herbivory	1	0.007	0.007	0.01	0.906
		Patch Type	1	8.403	8.403	18.10	0.000
	2006	Competition	1	1.242	1.242	1.12	0.294
		Microsite	1	4.865	4.865	4.38	0.040
		Herbivory	1	17.236	17.236	15.54	0.000
		Patch Type	1	37.834	37.834	34.10	0.000
	2007	Competition	1	18.742	18.742	2.73	0.103
		Microsite	1	19.229	19.229	2.80	0.099
		Herbivory	1	111.38	111.38	16.23	0.000
		Patch Type	1	187.89	187.89	27.38	0.000
%Low vigor	2007	Competition	1	3250	3250	1.05	0.310
		Microsite	1	10244	10244	3.29	0.074
		Herbivory	1	22067	22067	7.10	0.01
		Patch Type	1	16482	16482	5.3	0.025
%High vigor	2007	Competition	1	1298	1298	10.16	0.002
		Microsite	1	2750	2750	21.52	0.000
		Herbivory	1	2494	2494	19.52	0.000
		Patch Type	1	1973	1973	15.44	0.000
%Herbivore damage	2007	Competition	1	28.4	28.4	0.16	0.69

Table 4 (continued). General Linear Model tests of effects for treatments common to healthy and dieback patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of variation	df	SS	MS	F	p
		Microsite	1	86.5	86.5	0.49	0.486
		Herbivory	1	468	468	2.66	0.108
		Patch Type	1	185	185	1.05	0.309
%Insect damage	2007	Competition	1	986	986	2.66	0.108
		Microsite	1	1072	1072	2.89	0.094
		Herbivory	1	23.4	23.4	0.06	0.803
		Patch Type	1	3707	3707	9.99	0.002
%Soil moisture	2006	Competition	1	5.164	5.164	0.73	0.395
		Microsite	1	1.054	1.054	0.15	0.700
		Patch Type	1	108.25	108.2	15.36	0.000
Soil moisture	2005	Competition	1	0.261	0.261	60.13	0.000
		Microsite	1	0.479	0.479	110.5	0.000

Healthy, Dieback, Eroded Patches

Soil nitrate and total organic matter were significantly higher in the dieback sites than in the healthy or eroded sites (Table 5). Clay content was lower in dieback sites than in healthy sites while sand content was significantly higher in the eroded and dieback sites than in the healthy sites (Table 5). Soil moisture was assessed gravimetrically in fall 2006 and was significantly higher in the dieback sites (7.3%) than in the healthy sites (4.7%; $p < 0.001$; Table 4).

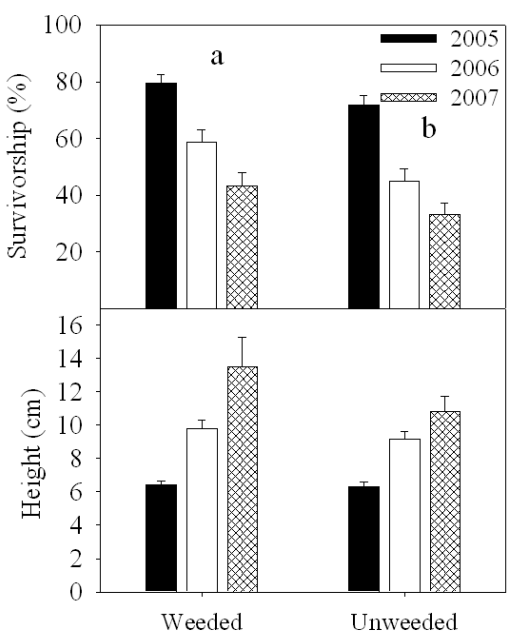

Figure 2. Mean survivorship and height for weeding (competition) treatments in healthy and dieback patches (n = 36). Differences in survivorship were significant for all years ($p < .05$), while height differences were not significant.

Results of the general linear model analyzing patch type and herbivory (fencing type) treatment are displayed in Table 6. There were no significant differences in acorn germination rates or total survivorship among the healthy, dieback and eroded patches (Table 6; Fig. 4). The combined dieback seedlings were significantly taller in all years ($p < 0.0001$, ANOVA, Table 6), and by 2007 were more than twice as tall (18 cm vs. 7 cm) as seedlings in healthy or eroded patches. Dieback ($\bar{x}$ = 19%) and eroded ($\bar{x}$ = 19%) sites were also assessed to have a greater percentage of high vigor seedlings compared to healthy ($\bar{x}$ = 4.6%) sites; however those differences were not significant (Tables 3, 6). Monitors also noted higher levels of insect damage in healthy sites ($\bar{x}$ = 70%) than in dieback ($\bar{x}$ = 56%) or eroded sites ($\bar{x}$ = 62%), however those differences were not statistically significant (Tables 3, 6). Survivorship of tree-tube seedlings was significantly higher than fenced seedlings only in 2007 and there were no interaction effects, although that effect was larger in dieback patches ($p = 0.007$, ANOVA). Similarly, tree-tube seedlings were

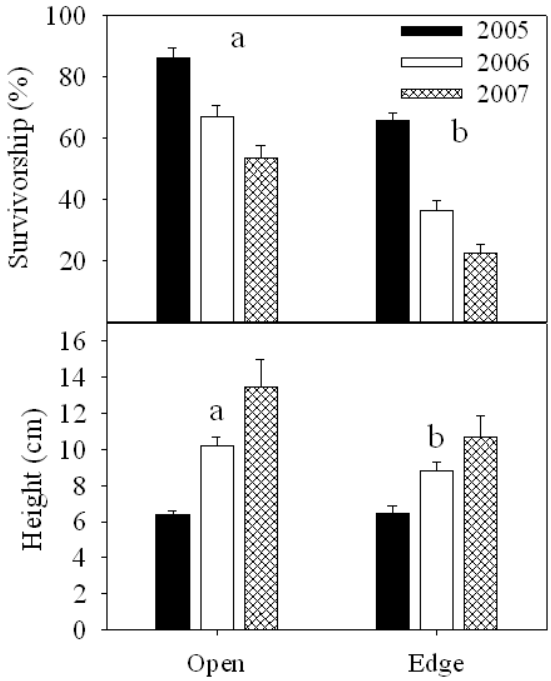

Figure 3. Mean survivorship and height of open grown and canopy edge seedlings from healthy and dieback patches (n = 36). Differences in total survivorship were significant all years ($p < .001$) and differences in height were only significant in 2006 ($p < .05$).

significantly taller than fenced seedlings in 2006 ($p < 0.019$) and 2007 ($p < 0.012$, ANOVA, Table 6).

DISCUSSION

Initially, herbivory, annual grass competition, and dieback were hypothesized to be the driving forces in the scrub oak ecosystem of Catalina Island. Our weeding and herbivory (fencing type) treatments were designed to evaluate the importance of these factors. Factors such as planting microsite (open field vs. canopy edge) and planting method (tree-tubes vs. fencing) were added to our research to supplement future restoration and management planning decisions. Results to date suggest that microclimate characteristics associated with open-grown and tree-tube protection have statistically and biologically more significant benefits to scrub oak seedling survivorship in their first three years than the fencing or the weeding treatment implemented in this study. Seedlings protected by tree-tubes had higher survivorship and growth in all relevant comparisons; and open-grown seedlings had at least twice the survivorship of canopy-edge seedlings in all relevant comparisons, even though height differences were insignificant.

Importance of Herbivory and Competition with Annual Grasses to Regeneration

Although numerous other studies have demonstrated significant enhancement of oak growth when seedlings were protected from deer browsing (Swiecki et al. 1997; Harvey 1989; Tyler et al. 2008), we found only minimal positive impacts of fencing out large herbivores. Indeed, herbivory by non-native deer and bison did not affect acorn germination or growth of small seedlings: we saw only a 6% increase in seedling survivorship between unfenced and fenced seedlings. Average seedling height among all seedlings, however, is just 5 cm, which means seedlings are still hidden within the annual grass canopy and less vulnerable to the impacts of

Table 5. Soil properties (nutrients and texture) compared between patch types (healthy, dieback, and eroded (for open field collected samples only)); and compared between open and edge sites across healthy and dieback plots. a/b notation used to signify significant differences; no letters indicate insignificant differences: $p < 0.05$.

	Organic %	P-P04 ug/g	N-NH4 ug/g	N-N03 ug/g	Clay %	Sand %	Silt %
Healthy (n=10)	1.27 a	4.19	2.26	1.67 a	18.14	40.6 a	41.2 a
Dieback (n=10)	2.02 b	3.16	2.05	14.3 b	7.6	50.6 ab	41.7 a
Eroded (n=10)	1.15 a	3.9	4.2	2.4 a	14.73	60.5 b	24.7 b
Open (n = 20)	1.65 a	3.67 a	2.16 a	7.99	12.9	45.7	41.5
Edge (n=20)	2.55 b	6.19 b	3.69 b	12.15	11.8	52.4	35.8

Table 6. General Linear Model tests of herbivory and patch type effects for open, unweeded treatment combinations in healthy, dieback, and eroded patches. Results for interaction terms are not presented unless significant.

Response variable	Year	Source of	df	SS	MS	F	p
Germination	2005	Herbivory	1	238.1	238.1	1.8	0.19
		Patch type	2	166.0	83.0	0.63	0.542
Survivorship	2005	Herbivory	1	65.8	65.8	0.17	0.688
		Patch type	2	707.8	353.9	0.89	0.426
	2006	Herbivory	1	1254	1254	2.11	0.161
		Patch type	2	802	401	0.67	0.520
	2007	Herbivory	1	4001	4001	8.91	0.007
		Patch type	2	501.6	250.8	0.56	0.580
Height	2005	Herbivory	1	0.117	0.117	0.67	0.421
		Patch type	2	5.86	2.93	16.92	0.000
	2006	Herbivory	1	4.51	4.51	6.44	0.019
		Patch type	2	25.59	12.79	18.29	0.000
	2007	Herbivory	1	18.64	18.64	7.67	0.012
		Patch type	2	71.10	35.55	14.62	0.000
%Low vigor	2007	Herbivory	1	2232	2232	5.76	0.026
		Patch type	2	573.2	286.6	0.74	0.490
%High vigor	2007	Herbivory	1	26.3	26.3	0.10	0.749
		Patch type	2	1240	620	2.47	0.106
%Herbivore damage	2007	Herbivory	1	72.2	72.2	1.04	0.318
		Patch type	2	191.5	95.7	1.38	0.272
%Insect damage	2007	Herbivory	1	1915	1915	3.15	0.090
		Patch type	2	794	397	0.65	0.530

browsing by large herbivores. Deer and/or bison browsing may play an important role as seedlings enter the sapling stage and are more visible to these herbivores. Indeed Tyler et al. (2008) showed that deer browsing of coast live oak seedlings in Santa Barbara County, California, increased in importance as seedlings aged.

Weeding treatments did not confer significant benefits to growth; however, weeded sites had higher acorn germination rates and consistently higher survivorship than unweeded sites. These results are more or less consistent with previous studies that have demonstrated competitive effects of annual grasses on seedling survivorship or growth in California oaks (Gordon and Rice 1993; Danielsen and Halvorson 1991). Although statistically significant, these differences were not as large as those between open and edge or tree-tube and unfenced treatment comparisons. Just 30% more weeded seedlings (43% versus 33%) were alive in 2007 than unweeded seedlings, while 100% to 200% more open-grown seedlings survived than their canopy-edge counterparts. The only significant differences in acorn germination results were associated with increased light levels: weeded treatments and open grown treatments which both had significantly higher acorn germination rates. These results suggest that annual grass effects may begin with reduced germination and continue with reduced survivorship. The effects of the weeding treatment on growth might have been stronger if there had been more frequent weeding through the spring.

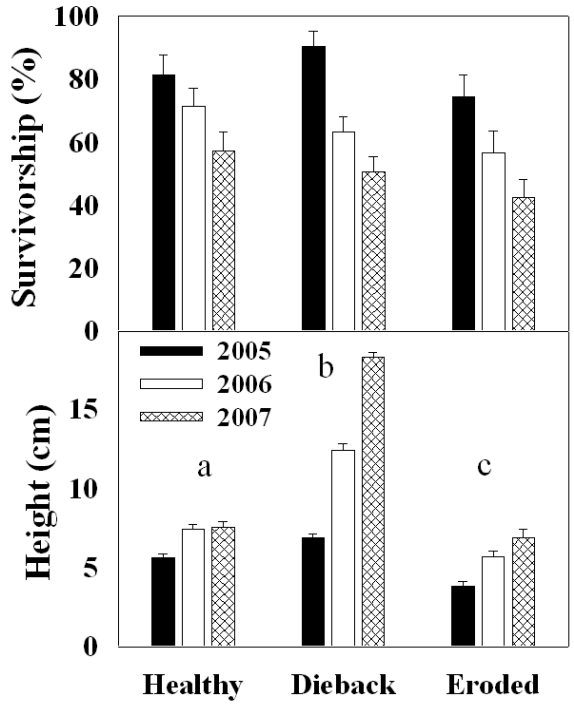

Figure 4. Mean survivorship and height by patch type for open grown, herbivore-protected (fenced or tree-tube) seedlings from unweeded treatments in healthy (n = 8 (1 block burned)), dieback (n = 10) and eroded (n = 10) patches. Differences in survivorship were not significiant. Differences in height were significant in all years ($p < 0.0001$).

Role of Microclimate and Patch Type

Survivorship of seedlings planted in the open was 120% higher (48% vs. 20%) than seedlings planted in edge locations (Fig. 3). This high survivorship was not due to nutrients because soil nutrients were higher in canopy-edge locations (likely due to increased woody debris) compared to open microsites. If light and water were limiting factors for canopy-edge seedlings, one might expect these seedlings to be shorter and possibly have lower vigor than their open-grown counterparts; however those differences were not apparent. An alternative explanation for significantly lower survivorship but equal heights between canopy-edge and open locations is that canopy-edge seedlings have disproportionately higher soil pathogen loads under conspecific canopies or by oak-specific insect herbivores; as found by Augspurger (1983) and Wada et al. (2000). We investigated this hypothesis by carefully unearthing dead seedlings from open and canopy-edge locations in both healthy and dieback patches in October 2007; the seedlings along with soil samples were sent to the soil pathogen laboratory at the University of California–Davis to test for colonization by soil pathogens or presence of soil-borne spores. Although slightly more identifiable soil pathogens (*Pythium* and *Mortierella*) were associated with dieback and canopy-edge seedlings, the results were inconclusive and unknown fungal hyphae were associated with all seedlings. Interestingly, no spores were found in any of the soil samples after baiting and incubation. Further tests of soil pathogen loads on seedlings should be pursued when the soils have been naturally wetted and fungi are active.

Interestingly, the patch type (dieback, healthy, eroded) did not significantly affect initial germination or survivorship although the seedlings growing in the dieback sites were significantly taller, particularly when grown in tree-tubes. These results demonstrate that factors other than soil pathogens or site-specific soil characteristics are causing the dieback phenomenon observed on Catalina Island. The results also indicate that restoration can occur in all patch types to re-establish oak trees in areas that are currently bare. Furthermore, these results suggest that dispersal of acorns to suitable germination sites out in the open may be a key limiting factor and an important, low-cost restoration strategy.

Why is Dieback Occurring?

The lack of difference in survivorship between the patch types (healthy, dieback, eroded) and lack of conclusive evidence about pathogens suggest the dieback phenomenon is more likely a result of senescence of old existing oak clones which have been unable to establish new basal sprouts due to browsing. The oaks may be more prone to death in areas where goats preferentially browsed on basal shoots over their 174-year tenure on the island (1827–2000). This repeated clipping of basal sprouts may have effectively drained the carbon stores in the underground storage rhizome (Langley et al. 2002; Canadell and Lopez-Soria 1998). According to growth ring counts from cores and cross sections, the maximum life span of an individual scrub oak stem is 100 to 115 years (de Gouvenain and Ansary, in press); however, as a multi-trunked organism, each scrub oak tree (or

clone) may live longer as new basal branches replace senescing ones to form a "continuously regenerating canopy in the absence of herbivory" (Keeley 1992). The dieback patches are first detectable in early historical photos from the 1950s on the west end of the island and may reflect historical patterns of feral ungulate, primarily goat, activity. If the remaining trees can be protected from current deer browsing pressures, they may still have sufficient energy stores to regenerate new basal sprouts that could create vigorous canopies much faster than could new germinants.

A Strategy for Oak Restoration

Tree-tubes are known to increase apical stem growth and provide more consistent and longer growing conditions (Ponder 1994). Significantly more tree-tube seedlings were classified as having high vigor (11%) relative to fenced (2%) and unfenced (1%) seedlings. This effect is stronger where organic, nutrient-rich soils exist. All seedlings growing in the nutrient-rich soils of dieback patches were taller than those in healthy or eroded patches; however that benefit was most strongly seen in tree-tube seedlings. Tree-tubes could help seedlings grow out of the browse line and produce acorns sooner by stimulating apical growth, particularly in loamy, nutrient-rich soils. Given the high survivorship provided by the microclimate within tree-tubes and the overall suitability of all patch types and open areas, it would seem that the highest rate of return for planting effort would be to establish large patches of oaks from acorns planted in tree-tubes in open areas.

Although survival of 22% of the unfenced, unweeded control seedlings suggests that dispersal to suitable germination sites may be more limiting than herbivory; these seedlings are still shorter than surrounding annual grasses, and one cannot predict what percentage will make it to sapling or reproductive age (Manuwal and Sweitzer 2006). Although planting acorns without weed or browsing protection across the landscape (e.g., acting as a good disperser) might be significantly cheaper, investing in tree-tubes could produce a threefold increase in survivorship (63% vs. 22%). Also, the long-term prognosis for unprotected seedlings cannot be determined from three years of data. Clearly, however, fencing alone does not confer the kind of benefits offered by tree-tubes. Where a stand of oaks is desired quickly, tree-tubes may play an important role in helping seedlings grow above browse height.

If senescence caused by herbivore pressure on basal sprouting of adult plants is the cause of the dieback phenomenon, which recent examinations of historical photos suggest has been ongoing since the first aerial photographs in 1943, then the complete lack of saplings or regenerating basal sprouts is an alarm call for protection of this threatened scrub oak ecosystem. It portends an island-wide decline in mature oaks with depleted energy stores for regeneration and indicates an immediate need for animal removal or construction of exclosures around existing oaks to allow for basal regeneration of canopy stems before stand-level senescence becomes a broader, island-wide phenomenon.

The apparent lack of dispersal agents and the role that annual grasses may play in limiting availability of suitable germination sites for acorns that roll downslope or otherwise naturally disperse suggest that we cannot just wait for these disappearing stands to regenerate on their own. Human "dispersal" to canopy openings in good rain years and the use of tree-tubes may together expand this woodland to its original extent.

Future Research

Further research suggested by this study includes following this trial as the seedlings grow beyond the protection of the grass canopy to fully evaluate the effect of bison and deer on the growth of seedlings to saplings. This will have implications on the likelihood of stand expansion under current browsing pressures. A study correlating the relationship between the diameter of stems and their ability to bring photosynthate back to the underground storage tubers, as well as a study relating the diversity and size of the stems of trees and available energy and nutrient stores in underground storage tubers, would help us validate the hypothesis that the dieback phenomenon is a result of years of browsing pressure. A field study examining the range of sizes of stems in trees on the landscape will help assess the potential for ecosystem collapse under the current browsing regime.

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PATTERNS IN POST-GRAZING VEGETATION CHANGES AMONG SPECIES AND ENVIRONMENTS, SAN MIGUEL AND SANTA BARBARA ISLANDS

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Abstract—Nonnative herbivores were removed from San Miguel and Santa Barbara islands by the late 1970s and early 1980s. To characterize post-grazing vegetation change while controlling for variable climate, we analyzed long-term (1984–2002) vegetation transect data on both islands for cover trends of individual plant species and correlations of plant community composition with physical site characteristics. We also analyzed species cover and environmental data from 28 vegetation plots sampled in 1983 and 2002 on San Miguel Island. Regression modeling of transect data for both islands and paired t-test analyses of San Miguel plot data found that both natives and exotics of various life histories have increased significantly since the early 1980s while other taxa and functional groups have declined. Species trends are generally consistent across different plant communities and both islands. Ordinations of species and environmental data indicate that soil texture and related soils variables are the environmental parameters most consistently correlated with species composition. Exotic grass cover is associated with fine-grained soils and native species cover with coarse-grained substrates. Results can be used to direct and prioritize native vegetation restoration and weed control efforts by indicating which native species are recovering and which exotic species are declining without intervention, and which environments are most likely to require active restoration efforts.

INTRODUCTION

The Channel Islands were used as ranches throughout the past two centuries, much like mainland California. Herbivory and farming quickly reduced native insular vegetation to remnant communities persisting in relatively inaccessible sites, within a matrix of non-native annual grassland. The five northernmost islands are now part of Channel Islands National Park, managed for recovery and conservation of native island ecosystems. One of the first large-scale management actions taken by the National Park Service was the eradication of nonnative herbivores from San Miguel and Santa Barbara islands. On San Miguel, sheep were reduced in number throughout the mid-twentieth century and eliminated in 1966; the last nonnative herbivores (feral burros) were removed ca. 1977 (Roberts 1991). Sheep were removed from Santa Barbara in the late 1920s and the last nonnative herbivores (feral rabbits) were eliminated in 1981 (Rugel 1995). A management expectation was that natural succession would result in the spread of native plants from their refugia in response to the release from herbivory.

Indeed, field observations and repeat photography show evidence of vegetation change since removal of herbivores on the Channel Islands (Philbrick 1972; Brumbaugh 1980; Johnson 1980; Philbrick and Haller 1995; Santa Cruz Island Foundation 2004). This change appears to vary spatially and temporally, similar to the findings of mainland studies (e.g., Hobbs 1983; Hobbs and Mooney 1986; Young et al. 1999; Allen et al. 2002; Zavaleta et al. 2001; Stromberg et al. 2007). For example, some areas that were dominated by exotic annual grasses 20 or 30 years ago now host dense native shrub stands with minimal exotic species cover, while other exotic communities sharing a similar land use history appear to have changed very little. Recent studies have shown that weather has a strong influence on demographic performance of several rare island endemic taxa (Levine et al. 2008) but the relationship between weather and plant

community change on the islands is not well documented. Channel Islands National Park initiated long-term vegetation monitoring on San Miguel Island in 1983 and Santa Barbara Island in 1984, to document plant community change in response to the removal of grazing animals (Halvorson 1994; Johnson and Rodriguez 2001). We used these data for 1983/84 through 2002 to investigate vegetation change on those islands. Our goals were to investigate change over time in species' cover, after accounting for species' individual responses to fluctuations in precipitation. Because observations indicated that change occurred at various rates across different landscape positions, we also investigated the relationship of environmental factors, such as soils, to vegetation pattern.

METHODS

Study Area

San Miguel is a 37 km^2 island underlain by Cretaceous, Tertiary, and Quaternary marine sediments, volcanics, and eolianite deposits (Johnson 1967, 1980). Santa Barbara, the smallest Channel Island at 2.6 km^2, is predominantly Miocene basalt with localized veneers of Quaternary sediments (Vedder and Howell 1976). The region has a maritime Mediterranean climate, with nearly all precipitation falling between November and April. The 30-year mean annual precipitation for the period 1971–2000 at Oxnard, California, the nearest climate station to the islands, was 397 mm (Western Regional Climate Center 2003). Because the region has a semiarid climate and is affected by El Niño Southern Oscillation events (Schoenherr et al. 1999), annual precipitation fluctuates considerably. San Miguel's climate is cooler and foggier than Santa Barbara's because of the island's position in the cold outer waters of the California Current; Santa Barbara Island is in the warmer waters of an eddy flowing up from the south.

Vegetation Sampling with Plots

San Miguel Island vegetation was sampled in 1983 on 85 unmarked plots as part of an effort to classify island plant communities. Plots were of varying dimensions, generally 1200–3600 m^2. Cover for each species on a plot was visually estimated within the five cover classes of the Braun-Blanquet scale (Class 1=1–5% cover, 2=5–25%, 3=25–50%, 4=50–75%, 5=75–100%; Mueller-Dombois and Ellenberg 1974). In 2002, we resampled 28 plots that had sufficient photographic and other documentation for reliable relocation. Species cover was visually estimated using the five cover classes of the Braun-Blanquet scale. Within each plot we established and sampled a 5 x 20 m subplot. The subplots have no 1983 counterpart, but they simplify analyses of current vegetation by eliminating potential effects of variable plot size on species composition. We collected environmental site data and documented plot locations by photography, global positioning systems, topographic maps, and aerial photos.

Vegetation Sampling with Monitoring Transects

The National Park Service (NPS) established permanent vegetation monitoring transects on San Miguel and Santa Barbara islands in 1984 and has sampled them annually most subsequent years (Johnson and Rodriguez 2001). Most transects are 30 m in length; several transects on Santa Barbara Island are 20 m or 40 m. Point poles are used to determine every species present at points on 30 cm intervals along the transect. Data from 1984 through 2002 were used for this study.

Environmental Data

Environmental variables measured or estimated on all plots and transects in 2002 include slope, aspect, and the categorical variables slope shape, topographic position, and soil drainage. Aspect was converted to a heat load index (McCune et al. 2002). Elevations were estimated from USGS topographic quadrangles. Percent bare ground and percent cryptobiotic crust cover were visually estimated in the field at plot sites in 2002. Percent bare ground is routinely measured by point-count on transects.

The upper 10 cm of soil was sampled in 2002 at all transect and plot sites via 4-point composites. Samples were oven-dried, passed through a 2-mm sieve, and analyzed by Brookside Laboratories of New Knoxville, Ohio, for soil texture (percent sand/silt/clay), bulk density, and a standard suite of soil chemistry parameters including pH, electrical conductivity, percent organic matter, cation exchange capacity, major cations and anions, and

macro- and micronutrients. Soil nitrogen was measured via NO_3 and NH_4 concentrations and estimated nitrogen release (ENR). Soil analytical results for San Miguel transect 18 were also used for adjacent transect 11, which was replaced by transect 18 in 1994. Transect 16 was not sampled due to archaeological protection constraints; soil analytical results for transect 13, which is on a very similar sand substrate and geomorphic position about 2 km distant, were also used for transect 16.

Species Cover Trend Analysis

Statistical analyses were conducted using R 1.9.1 (R Development Core Team 2004) unless otherwise noted. Taxonomic nomenclature follows the USDA Plants database (USDA NRCS 2001). Analyses were designed to determine which species experienced significant changes in cover over time while accounting for effects of precipitation, and to show the magnitudes and directions of the changes. San Miguel plot and transect datasets were analyzed separately because of differences in the data structure and data collection methods.

The paired difference in cover class (the number of cover classes spanned by the change between 2002 and 1983) on each San Miguel plot and the mean paired difference over all plots were calculated for species present on at least eight plots in either or both years. A paired t-test determined whether a species' mean cover class was significantly different in 2002 vs. 1983 ($\alpha = 0.05$). For comparison, we also used the nonparametric Wilcoxon's signed rank test to test for significant changes in cover class among species. In both analyses, multiple testing (multiple species present on a given plot) was accounted for using Benjamini and Hochberg's (1995) step-up procedure to control the false discovery rate (FDR) at 5%. The FDR is defined as the expected percentage of significant tests that could be falsely significant.

For each San Miguel and Santa Barbara transect in each year, the point count for each species was converted to percent cover by dividing the number of point-interceptions for the species by the total number of points on the transect. To limit multiple testing and focus on common species, analyses were confined to species present at least two years of the monitoring period, with a minimum cover of 4% for at least one of the years. To account for multiple tests, Benjamini and Hochberg's (1995) step-up procedure was used to control the FDR at 5%.

We used a linear mixed-effects regression modeling approach to determine which species experienced significant changes in percent cover over time. We used a model structure that is suitable for time-series data such as the transect data because it automatically accounts for autocorrelation and heteroscedasticity (Singer and Willett 2003), characteristics that can make ordinary least-squares regression inappropriate for repeated-measures data. We used annual water-year (July to June) precipitation as a covariate to account for its contribution to variability in species cover, because species do not all respond similarly to precipitation variability. Water-year precipitation was calculated from monthly totals for the Oxnard NOAA reporting station (Western Regional Climate Center 2003). A moving three-year average for water-year precipitation was used because plant cover response appears to be a function of several years' precipitation rather than just the current year.

Each island's data were analyzed separately. The basic framework for the regression model can be expressed as:

$$Y_{ijk} = \alpha_{0ij} + \alpha_{1ij}TIME_{ijk} + \alpha_{2ij}PPT_{ijk} + \varepsilon_{ijk}$$

where TIME is the number of years since 1984 (i.e., 1984 = 0), and PPT is total water-year precipitation for year k. The cover value (Y) for species *j* on transect *i* at time *k* is due to the initial cover at time 0 (α_{0ij}, the intercept), the partial rate of change in cover with respect to time, the partial rate of change in cover with respect to precipitation, and random error. Each species' regression coefficient for the time term (α_1) represents its cover trend (the percent change in cover class category per year). The variable PPT was included in the model to remove the variation due to annual precipitation from the analysis, so we could examine the temporal trend in vegetation cover independent of precipitation.

In linear mixed-effects modeling, comparative versions of models can be constructed that vary in which parameters (intercepts and regression coefficients) are fixed at mean values (in this case, the mean value for a given species over all transects on which it occurs), and which parameters are random (allowed to assume the actual values on

each transect). Our reported results are from a model in which the intercept is random but both time and precipitation coefficients are the mean values across all transects. However, a mean time trend may not be meaningful if a species' cover trend differs markedly among transects, increasing over time on some transects and decreasing on others. To check whether mean time coefficients are reasonable representations of species' cover trends, we fitted a second model which differed from the first in allowing the time coefficient to be random, and compared the two models to determine whether any species have a significant random time effect, indicating heterogeneity in cover trend among transects. For species that did exhibit heterogeneity among transects, we examined model results and raw data to evaluate the source of heterogeneity and to assess whether a mean value across transects was a meaningful representation of cover trend.

To assess the generality of trends, we combined data from both islands and used a variation of the model described above to test whether species' temporal trends are significantly different between the two islands. The combined dataset included only species present on transects on both islands at the specified minimum-presence levels. Additionally, four similar congeneric pairs, such as *Eriogonum grande* v. *rubescens* on San Miguel Island and *E. giganteum* on Santa Barbara Island, were renamed by genus only, so that each pair was treated as the same taxa in the analysis. *Astragalus*, *Calystegia*, and *Claytonia* were the other genera treated this way. Multilevel models were fit with and without a dummy variable that identified the island on which a transect occurs. An analysis of deviance assessed whether inclusion of the island term changed results significantly for any species. FDR significance (α = 0.05) was calculated to correct for multiple testing.

Species Composition and Environmental Correlations

Species composition patterns and correlations with environmental variables were assessed using nonmetric multidimensional scaling (NMS) ordinations in PC-ORD 4.32 (McCune and Mefford 1999). NMS solutions are graphically displayed in ordination diagrams showing the vegetation plots in two-dimensional ordination space; the proximity of plots indicates the degree of species-compositional similarity between them. The Sorenson (Bray-Curtis) distance measure was used to calculate the dissimilarity matrix. We evaluated the acceptability of an NMS solution by its final stress and instability, using criteria of final stress <17, per Clarke's (1993) rules of thumb, and final instability <0.001 (McCune et al. 2002). Effectiveness of NMS solutions was assessed by calculating the proportion of variance in the original data that is represented by each ordination axis. The metric is the coefficient of determination (r^2) between distances in the original data and distances in ordination space. An ordination solution was considered effective when at least 50% of the variance was represented by two ordination axes (McCune et al. 2002).

Ordinations included a secondary matrix of the environmental variables measured or estimated at plot and transect locations. Ordination correlates environmental variables with ordination axes that represent gradients of species composition, calculating Pearson's r^2 to describe the linear relationship between environmental variables and ordination scores, and Kendall's tau to describe the rank relationship. Pearson's r^2 is the proportion of variance in a sample's position on an ordination axis that is explained by a given environmental variable.

Data for San Miguel plots, San Miguel transects, and Santa Barbara transects were ordinated separately. To assess whether species composition and environmental correlations are changing over the time, we ordinated data from a recent monitoring year (1998–2002), combined early (1983/84) and recent years, and various combinations of multiple years throughout the 19-year period. We also ordinated data from a very dry year (1990) and a very wet year (1998) to evaluate whether water-year precipitation affects species composition and environmental relationships. Multiple-year analyses included only transects present in each of the subject years; several sporadically sampled transects on both islands were eliminated from these analyses.

The San Miguel plots were only sampled twice, in 1983 and 2002. For current vegetation patterns, we ordinated data from the 5 x 20 m subplots we established in 2002 within the original plots. The subplots have the advantage of standard size. To combine 1983 and 2002 data, we used 2002 data from the larger plots (of the 1983 dimensions). Because the plots are of varying sizes, we included

plot size as a quantitative variable in the secondary matrix to assess its correlation with species composition (i.e., the extent to which varying plot sizes may have affected species composition via sampling effect).

RESULTS

Species Cover Trends on San Miguel Plots

The combined 1983 and 2002 data included 93 species; 29 met minimum presence criteria and were included in the analysis. Eleven of the 29 species had significant differences in Braun-Blanquet cover class categories between 1983 and 2002 (Table 1). The FDR significance level of 5% indicates that less than one significant test (5% of 11 tests) could be spurious, suggesting all tests remain significant after accounting for effects of multiple testing. The nonparametric Wilcoxon signed-rank test produced very similar results.

Species that significantly increased include the native shrubs *Lupinus albifrons*, *Coreopsis gigantea*, and *Baccharis pilularis*, the native grass *Distichlis spicata*, and the native thistle *Cirsium occidentale*. The annual grass *Bromus hordeaceus* was the only exotic species that increased. Only one native species, the subshrub *Malacothrix incana*, decreased. Exotic species that decreased in cover are the annual grass *Hordeum murinum*, a species common in saline waste areas; the herbs *Melilotus indicus* and *Sonchus oleraceus*, and the salt-tolerant subshrub *Atriplex semibaccata*.

Species Cover Trends on San Miguel and Santa Barbara Transects

Graphical examination of modeling results for species with significant heterogeneity in temporal cover change among transects found that the mean time trend is generally an appropriate representation of species trend. For example, Figure 1 compares observed temporal trends of *Eriogonum giganteum* v. *compactum* cover for the three transects on which

Table 1. Significant paired t-test and Wilcoxon signed-rank test results for San Miguel plots. Species with significant ($\alpha = 0.05$) mean change in Braun-Blanquet cover class category from 1983 to 2002 are listed in descending order of direction and magnitude of change, using paired t-test results. N = number of plots on which species occurs. Lifeform/life history: P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Mean change in cover class	*p*	Wilcoxon *p*
Bromus hordeaceus soft chess	A. grass*	10	1.500	0.001	0.004
Lupinus albifrons silver lupine	P. shrub	11	1.000	0.002	0.008
Distichlis spicata saltgrass	P. grass	18	0.778	0.015	0.026
Coreopsis gigantean giant coreopsis	P. shrub	13	0.615	0.005	0.016
Baccharis pilularis coyote brush	P. shrub	23	0.478	0.008	0.019
Cirsium occidentale California thistle	P. forb	24	0.292	0.016	0.039
Sonchus oleraceus sow thistle	A. forb*	24	-0.417	0.009	0.020
Malacothrix incana dunedelion	P. shrub	19	-0.632	0.001	0.003
Atriplex semibaccata Australian saltbush	P. subshrub*	13	-0.769	0.002	0.011
Melilotus indicus yellow sweetclover	A. forb*	18	-0.778	0.001	0.003
Hordeum murinum foxtail	A. grass*	8	-1.375	<0.001	0.008

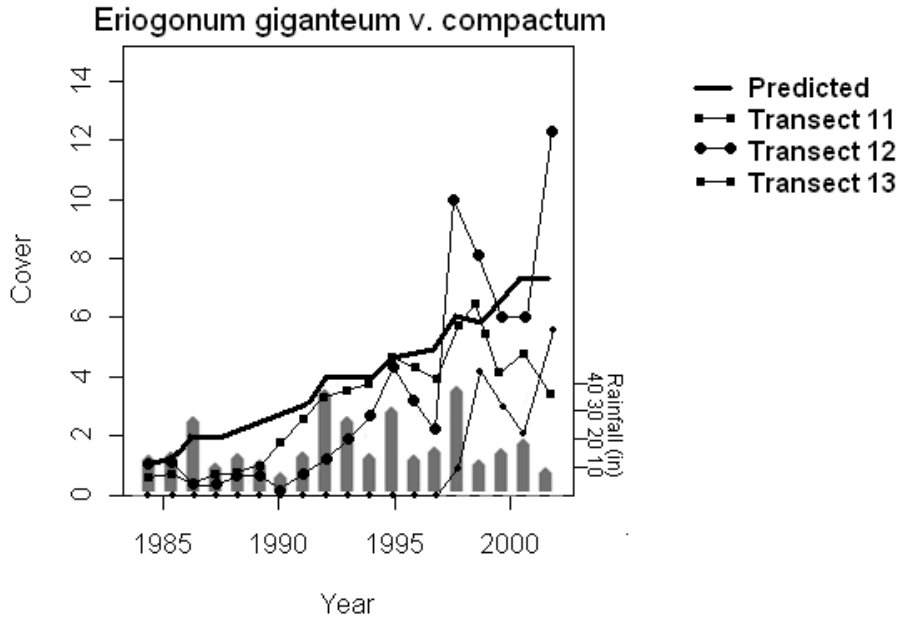

Figure 1. Observed and predicted trends of percent cover for *Eriogonum giganteum* v. *compactum* from 1984 to 2002. Bulleted lines represent observed trends on the three Santa Barbara Island transects on which the species occurs. The solid line represents percent cover estimated by the multilevel regression model, averaged over all three transects. Bars at the bottom of the graph indicate annual variation in precipitation. Percent cover generally increases over time on all transects; the heterogeneity is due primarily to differences in the magnitude of the increase rather than opposing trends.

it occurs, with the mean temporal trend predicted by the multilevel regression model. Variability in percent cover due to annual precipitation has been accounted for in the model, resulting in a smoother temporal trend line compared to observed values. This figure illustrates a typical example of a species that displays significant heterogeneity among transects. However, where heterogeneity among transects was found, it generally reflected large differences in initial cover that affected the magnitude of change, rather than divergent trends. For example, some species' cover declined on all transects, but could not decline as much on transects where initial cover was low.

San Miguel transects captured 103 species, of which 79 met minimum presence criteria. Twenty-three of the 79 species had significant ($\alpha = 0.05$) temporal trends (Table 2). The FDR ($\alpha = 0.05$) suggests that one of the 23 significant tests could be spurious. Positive values of α_1 indicate that seven native species (four shrubs and three herbs) and three exotic species exhibit significant increases in cover (Table 2). Negative values of α_1 indicate that eight native species and five exotic species decreased in cover (Table 2), including both native vines (*Calystegia macrostegia* and *Marah macrocarpus*), salt-tolerators (*Hordeum murinum* and both species of *Atriplex*), and several species that tend to increase under grazing pressure (exotic herbs *Erodium cicutarium* and *Medicago polymorpha* and the native cactus *Opuntia littoralis*). Most of the other declining species are associated with sand dunes and other open habitats.

Santa Barbara Island transects captured 67 species, of which 50 met minimum presence criteria for analysis. Thirteen of the 50 species had significant ($\alpha = 0.05$) temporal trends (Table 3). The FDR ($\alpha = 0.05$) suggests that all tests remain significant after accounting for multiple testing. Only three species, all native, increased in cover. The 10 decreasing species include five out of six salt-tolerators in the analysis: both *Atriplex* species, both *Mesembryanthemum* species, and *Suaeda taxifolia*. Other decreasing species include a native shrub, cactus, and grass, an exotic grass, and another exotic herb.

Table 2. Regression coefficients and *p*-values for species with significant temporal trends on San Miguel Island transects, ordered by direction and magnitude of temporal trend. α_1 is the regression coefficient for the partial rate of change in a species' percent cover due to time. α_2 is the regression coefficient for the partial rate of change in a species' percent cover due to annual precipitation. N = number of transects on which species occurs. Lifeform/life history: P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Time		Ppt	
			α_1	*p*	α_2	*p*
Eriophyllum confertiflorum golden yarrow	P. shrub	1	1.392	0.001	0.251	0.438
Coreopsis gigantea giant coreopsis	P. shrub	4	1.244	<0.001	0.877	0.008
Sisyrinchium bellum blue-eyed "grass"	P. forb	2	0.901	<0.001	0.086	0.526
Bromus hordeaceous soft chess	A. grass*	8	0.896	0.001	0.258	0.322
Carpobrotus chilensis iceplant; sea-fig	P. subshrub*	9	0.807	<0.001	0.449	0.030
Eriogonum grande v. *rubescens* red buckwheat	P. shrub	2	0.539	<0.001	0.138	0.042
Lotus dendroideus v. *dendroideus* deerweed	P. shrub	3	0.482	0.004	0.104	0.508
Dudleya greenei Greene's dudleya	P. subshrub	2	0.436	<0.001	0.097	0.358
Pterostegia drymarioides fairy mist	A. forb	3	0.182	0.004	0.334	<0.001
Sonchus oleraceus sow thistle	A. forb*	12	0.176	0.007	0.125	0.047
Atriplex californica California saltbush	P. subshrub	8	-0.260	<0.001	-0.048	0.469
Erodium cicutarium filaree	A. forb*	8	-0.428	0.001	0.160	<0.001
Medicago polymorpha bur-clover	A. forb*	8	-0.462	0.003	0.259	0.085
Marah macrocarpus wild cucumber	P. forb	4	-0.550	0.013	0.340	0.115
Atriplex semibaccata Australian saltbush	P. subshrub*	4	-0.602	0.010	0.440	0.050
Calystegia macrostegia island morning-glory	P. subshrub	7	-0.631	<0.001	0.222	0.174
Lupinus succulentus succulent lupine	A. forb	1	-0.862	0.005	-0.088	0.727
Malacothrix incana dunedelion	P. shrub	6	-0.987	<0.001	0.308	0.138
Bromus diandrus ripgut brome	A. grass*	12	-1.035	<0.001	0.614	0.004
Ambrosia chamissonis beachbur	P. shrub	1	-1.174	0.007	-0.144	0.696
Hordeum murinum foxtail	A. grass*	6	-1.424	<0.001	0.529	0.062
Artemisia californica coastal sagebrush	P. shrub	3	-1.684	0.008	0.410	0.411
Opuntia littoralis coastal pricklypear	P. shrub	2	-1.930	<0.001	-0.193	0.546

Table 3. Regression coefficients and *p*-values for species with significant temporal trends on Santa Barbara Island transects, ordered by direction and magnitude of temporal trend. α_1 is the regression coefficient for the partial rate of change in a species' percent cover due to time. α_2 is the regression coefficient for the partial rate of change in a species' percent cover due to annual precipitation. N = number of transects on which species occurs. P. = perennial, A. = annual, * = exotic.

Species	Lifeform/life history	N	Time		Ppt	
			α_1	*p*	α_2	*p*
Melica imperfecta Coast Range melic	P. grass	1	1.837	0.001	0.972	0.139
Opuntia littoralis coastal pricklypear	P. shrub	3	0.528	0.011	0.134	0.528
Eriogonum giganteum v. *compactum*	P. shrub	4	0.358	<0.001	-0.003	0.968
Malva parviflora cheeseweed	A. forb*	11	-0.265	0.008	0.036	0.799
Atriplex californica California saltbush	P. subshrub	3	-0.465	0.001	0.091	0.639
Hemizonia clementina island tarweed	P. shrub	5	-0.509	<0.001	0.301	0.103
Atriplex semibaccata Australian saltbush	P. subshrub*	16	-0.651	<0.001	0.735	<0.001
Opuntia prolifera coastal cholla	P. shrub	4	-0.820	0.003	-0.775	0.017
Suaeda taxifolia sea-blite	P. shrub	7	-0.914	<0.001	0.517	0.071
Bromus rubens red brome	A. grass*	17	-1.333	<0.001	1.907	<0.001
Mesembryanthemum nodiflorum small-flowered iceplant	A. forb*	2	-1.359	0.005	0.804	0.224
Mesembryanthemum crystallinum crystalline iceplant	A. forb*	12	-1.882	<0.001	0.473	0.106
Muhlenbergia microsperma littleseed muhly	A. grass	2	-4.578	0.001	1.567	0.044

Testing for Differences in Species Cover Trends between Islands

The two islands have 31 taxa in common on transects. Modeling of combined data for both islands found no significant difference in trends between islands for any of the 31 taxa, when multiple testing is accounted for via the FDR. Two species, *Chenopodium californicum* and *Opuntia littoralis*, have significantly different trends between islands before correction for multiple testing.

Species Composition and Environmental Correlations from Ordinations

All acceptable NMS solutions had three dimensions and were deemed effective, with 55–68% of the original data's variance explained by two axes. Species composition gradients and their Pearson's r^2 and Kendall's tau correlations with environment were similar in all ordinations for a given island, regardless of which years' data were used; species composition-environment

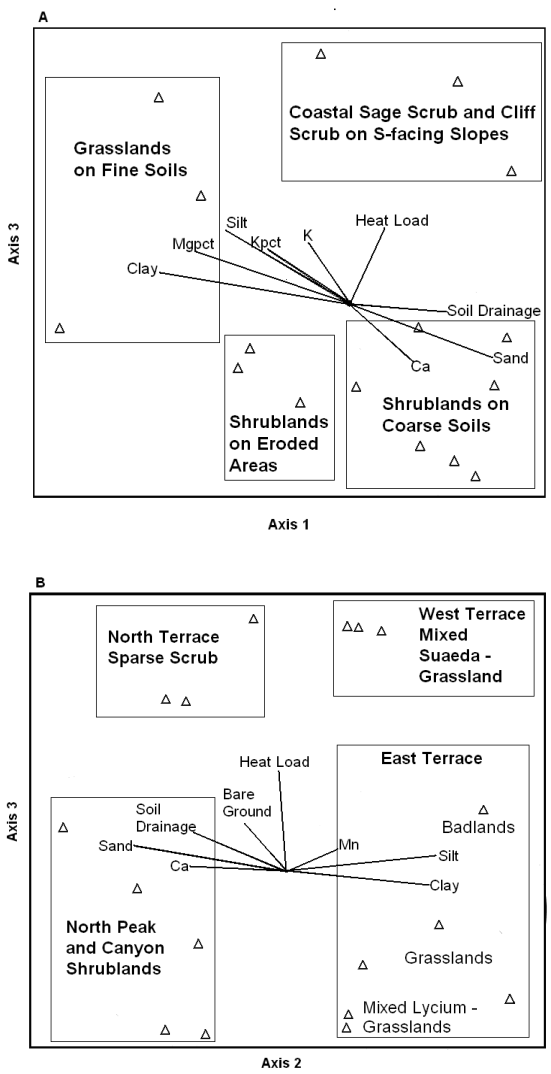

Figure 2. Nonmetric multidimensional scaling (NMS) ordinations of transect species data, with vectors showing relative strengths of Pearson's r^2 correlations with some environmental variables measured at the sites. a) San Miguel Island 2002 data, b) Santa Barbara Island 1998 data.

relationships do not appear to be changing over time or fluctuating with annual precipitation.

San Miguel plots and transects generally sort along two types of species compositional gradients: 1) grasslands (predominantly exotic) vs. native-dominated shrub vegetation, and 2) dense vegetation of any type on relatively deep soils vs. sparse vegetation on thin soils or erosion pavements (Fig. 2a). Most native-dominated shrub communities such as lupine, *Coreopsis*, and *Isocoma* scrub tend to group together despite differences in dominant species. Exceptions are coastal sage scrub and cliff scrub on south-facing slopes, which tend to group separately from other native communities, and *Baccharis* scrub and the few grasslands with a native graminoid component, which generally group with or near exotic grasslands. Ordination axes also reflect site environmental conditions, most commonly representing gradients between fine- and coarse-grained substrates and between warm/xeric sites such as south-facing slopes and cool/mesic sites such as canyons and north-facing slopes.

Santa Barbara transects generally group by geographic regions of the island: mixed shrub-grassland (*Suaeda taxifolia – Hordeum murinum*) communities on the west terrace, sparsely vegetated annual-rich low scrub communities on the north terrace near Arch Point, native shrub communities on North Peak and in canyons, and east terrace communities (Fig. 2b). Within the latter, three subgroups are evident: exotic grasslands, mixed shrub-(*Lycium californicum*) grassland, and a heavily eroded *S. taxifolia – H. murinum* badlands site. The east terrace sites share a large *Avena* component that appears to separate this group from the others. Similarly to San Miguel, ordination axes appear to represent gradients between fine- and coarse-grained substrates and between warm/xeric and cool/mesic sites.

On both islands, soil texture (percent sand, silt, and clay) and soil drainage are the strongest, most consistent environmental correlates with species composition, with Pearson correlation coefficients (r^2) up to 0.80 (Table 4). Native-dominated communities are associated with well-drained soils with high sand content, while predominantly exotic grasslands are associated with slower-draining soils with high silt and clay. These correlations are significant but weaker on San Miguel plots compared to the transects, possibly because sand dune habitats were underrepresented due to the difficulty of reliably relocating plots on shifting sands.

Major cations covary with soil texture and are also consistent, although generally weaker, correlates with species composition. High calcium is associated with native communities on coarse soils while magnesium, potassium, and, less consistently, sodium are associated with grasslands on finer-grained soils. Heat load is another frequently significant correlate, supporting the

Table 4. Pearson's r^2 correlation coefficients for environmental variables and NMS ordination axes (see Fig. 2) for 16 San Miguel Island transects, 2002 data; and 18 Santa Barbara Island transects, 1998 data. Variables with Pearson's $r^2 \geq 0.2$ are in bold.

	San Miguel		Santa Barbara	
	Axis 1	Axis 3	Axis 2	Axis 3
Sand	**0.63**	**0.23**	**0.67**	0.07
Silt	**0.42**	**0.24**	**0.59**	0.03
Clay	**0.80**	0.14	**0.52**	0.10
TEC	**0.23**	**0.28**	**0.48**	0.10
pH	**0.26**	**0.30**	0.02	0.02
OM	0.13	0.18	0.15	0.00
ENR	0.16	**0.33**	0.17	0.00
S	0.15	**0.32**	0.14	0.15
P	0.06	0.00	0.00	**0.39**
Ca	**0.28**	**0.30**	**0.44**	0.00
Mg	0.01	0.00	0.09	0.14
K	**0.22**	**0.26**	0.15	0.15
Na	0.11	0.03	0.01	0.17
Capct	**0.45**	**0.34**	**0.26**	0.02
Mgpct	**0.48**	**0.24**	**0.30**	0.04
Kpct	**0.35**	**0.27**	0.08	0.02
Napct	**0.66**	0.16	0.04	0.16
B	0.14	**0.25**	0.15	0.12
Fe	**0.24**	0.07	0.16	0.04
Mn	**0.26**	**0.26**	**0.25**	0.01
Cu	0.11	0.07	0.00	0.00
Zn	0.06	**0.32**	0.10	**0.35**
Al	**0.33**	0.12	0.14	0.08
EC	0.05	0.02	0.03	0.06
Cl	0.05	0.02	0.05	0.12
BulkDensity	**0.24**	**0.37**	0.08	0.01
NO3	**0.54**	0.00	0.05	0.07
NH4	0.16	0.06	0.02	0.13
CaCO3	**0.23**	**0.22**	0.01	**0.21**
Elev	0.07	0.01	0.01	0.05
Slope	**0.22**	0.03	**0.44**	0.01
HeatLoad	0.05	**0.34**	0.07	**0.37**
SoilDrainage	**0.80**	0.07	**0.62**	0.05
BareGr	0.00	0.03	**0.24**	0.16

observation of compositional sorting between warm/xeric sites and cool/mesic sites. Percent bare ground is a frequent correlate, reflecting compositional gradients between densely vegetated sites on deeper soils and more sparsely vegetated areas such as Arch Point on Santa Barbara and erosion pavements and sand dunes on San Miguel. Less consistent correlates include some soil chemistry variables such as pH, cation exchange capacity, sulfur, and some micronutrients, all of which appear to covary with soil texture. The macronutrients nitrogen and phosphorus generally have insignificant or inconsistent correlations with species composition.

DISCUSSION AND CONCLUSIONS

Many factors can affect species' trends, including changes in land use, environmental setting, and climate fluctuations. Precipitation is highly variable in a Mediterranean climate regime, and it can affect the relative abundances of species across years of high rainfall and drought, with some species exhibiting stronger responses than others to rainfall variations. Our analyses were designed specifically to look at change independent of precipitation effects on individual species abundances. Therefore, we included precipitation as a covariate in our analyses, to account for the effect of varying moisture in the analysis of species cover trend. Results (Tables 2 and 3) show that when species' varying responses to precipitation are accounted for, significant differences in cover trends among species still emerge. Future analyses will focus on species trends as they relate to precipitation and temperature fluctuations, for species life-history forms and other functional groups. Our results do show that species are responding individualistically over time, within the context of changing management and climate regimes. Post-grazing cover trends are significantly different among some species, and a given species' trend is generally consistent across all plots and plant community types in which it occurs. Species cover trends do not vary significantly between the two islands despite climatic, edaphic and land use differences, suggesting generality of trends for other Channel Islands and possibly coastal mainland

systems recovering from similar anthropogenic impacts.

Most species that increased significantly are native, particularly native shrubs. These include fast-growing wind-dispersed shrubs such as *Coreopsis gigantea* and *Baccharis pilularis*, and species such as nitrogen-fixers with traits that facilitate colonization of low-nutrient sandy and rocky substrates. *Eriogonum* species on both islands increased; this genus appears to be a successful early colonizer on damaged lands. Stylinski and Allen (1999) found that the common mainland buckwheat *E. fasciculatum*, along with a *Baccharis* species, were the only native shrubs that colonized heavily damaged southern California scrub communities after cessation of anthropogenic disturbance.

Despite general increases in native species cover, some native species did decline in the 18–19 years of censusing. Both native vines, *Marah macrocarpus* and *Calystegia macrostegia*, decreased significantly on San Miguel transects; possibly their niches overlap with the exotic subshrub *Carpobrotus*, which has a prostrate, sprawling habit and is increasing. Native shrubs *Ambrosia chamissonis* and *Malacothrix incana* and the native annual herb *Lupinus succulentus* are all colonizers of sand dunes and other open sites; their decline on San Miguel may be due to competition from nitrogen-fixing shrubs and/or *Carpobrotus*, or loss of habitat as sand dunes and other open sites created by grazing-induced erosion stabilize and revegetate. Declining forb and graminoid species on both islands are mostly exotic; increasers are mostly native. Declining exotic forbs on both islands were nearly all halophytes or species such as *Medicago polymorpha*, *Melilotus indica*, and *Erodium cicutarium* that are associated with grazing disturbance.

The decline of certain exotic taxa appeared to be associated with functional traits; specifically, saline tolerance. Exotic taxa associated with saline disturbed areas declined significantly on San Miguel (*Hordeum murinum*) or on both islands (*Atriplex semibaccata*, *Mesembryanthemum* spp), possibly indicating a reversal of soil compaction and concomitant decrease in soil salinity that can follow grazing cessation (Chaneton and Lavado 1996; Belsky and Blumenthal 1997). The decline of *Mesembryanthemum crystallinum* on Santa Barbara may be at least partially attributable to experimental removal projects conducted ca. 1987 near North and Signal peaks (Halvorson 1994; Rugel 1995). Although the projects presumably avoided the immediate vicinity of monitoring transects, they may have decreased the abundance of *M. crystallinum* propagules sufficiently to affect cover on the transects. The decline of *Hordeum murinum* on San Miguel is supported by photo evidence from the late 1970s showing dense *H. murinum* covering large areas that are currently dominated by native vegetation. Native halophytes displayed a more equivocal trend: *Suaeda taxifolia* decreased on Santa Barbara and *Atriplex californica* decreased on both islands, but the saltgrass *Distichlis spicata* increased on San Miguel plots.

We found that native and exotic communities segregated according to environmental characteristics. Correlation of environmental variables with vegetation composition supports field observations of the affinity between exotic grasslands and fine-grained, slowly draining soils and between native scrub communities and coarse, well-drained substrates. Major cations were also frequent correlates. An experimental approach would be required to disentangle the effects of major cations and soil texture and assess whether either or both have a causative relationship with species composition, but the stronger, more consistent correlation of soil texture suggests it is the primary driver of the relationship with species composition.

On both islands sites tend to also sort by heat load. On San Miguel, native communities tend to associate with cooler, more mesic sites and exotic grass cover with warmer, drier sites. This relationship is more equivocal in Santa Barbara ordinations, but repeat photography on the island provides some qualitative evidence of the association, showing more extensive native plant colonization on north-facing gully slopes while the opposite slopes are generally dominated by exotic grasses.

Coarse-grained substrates are often thought of as xeric from a plant's perspective; therefore, native island communities' apparent preference for sites with both lower heat load (i.e., lower xericity) and coarse-grained, well-drained substrates may seem contradictory. However, for the deeper-rooted perennials that dominate native island communities,

coarse-grained substrates are probably less xeric than slower-draining soils because more moisture can percolate to the natives' deeper rooting zones. In arid and semiarid climates, slower-draining soils are often effectively more xeric than coarse-grained soils due to higher evaporative loss of moisture retained near the surface (Wells 1962). This effect would be compounded in the presence of the shallow-rooted annual vegetation that dominates island exotic communities; the annuals can more thoroughly deplete moisture retained near the surface in slower-draining, fine-grained soils. This has been proposed as a mechanism by which exotic annual grasses outcompete native perennials in Mediterranean-climate communities (Kirkpatrick and Hutchinson 1980; Hobbs 1983; Vila and Sardans 1999), and is supported by experimental studies (Gordon et al. 1989; Melgoza et al. 1990; Eliason and Allen 1997).

Characterizing patterns of vegetation change can inform vegetation management and restoration efforts by identifying taxa and environments most in need of active intervention and providing evidence of factors that control native vegetation recovery. We have identified specific native taxa, such as *Coreopsis*, *Baccharis*, and *Eriogonum*, and groups with shared traits such as nitrogen-fixers, as successful colonizers needing less active intervention but perhaps having utility as nurse plants or site remediators in restoration efforts. Exotic species and functional groups can be prioritized for removal efforts based on their cover trends: exotic halophytes and many grazing-associated forbs are apparently decreasing on their own, while some exotics such as *Carpobrotus* on San Miguel are spreading.

Native perennial colonizers appear to be at greatest advantage on sites where well-drained soils or rocky, fractured substrates such as erosion pavements allow more percolation to deeper rooting zones. Active restoration is most likely to be needed on sites with fine-grained soils. Results from San Miguel, at least, also indicate that spontaneous native recovery is favored where aspect results in relatively lower moisture stress. Our results suggest that competition with exotic annuals for soil moisture is an important factor controlling native vegetation recovery. Fruitful avenues for further research include restoration experiments involving fog drip capture or other methods of altering soil moisture competition between native perennials and exotic annual vegetation.

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COLONIZERS, WAIFS, AND STOWAWAYS: ARRIVAL OF NEW PLANT SPECIES ON SANTA BARBARA ISLAND OVER A 30-YEAR PERIOD

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Abstract—Santa Barbara Island is a small island with an extensive history of botanical exploration. We report on floristic studies on the island that have spanned the last three decades, covering the period since the removal of introduced European rabbits from the island. In aggregate, these studies have surveyed this small island thoroughly, and have recorded a significant percentage of additions to the island flora. Over the course of this period, 32 plant species have been recorded that are new to Santa Barbara Island. Just over half of these are non-natives. A few of the new species, such as *Baccharis emoryi*, have only been found on the island as single, non-persisting individuals. Most of the non-natives were first recorded in the Landing Cove area of the island, along trails, or in other locations that suggest they were inadvertently transported to the island by people. Of the native species, nine are composites (family Asteraceae), and all appear to have arrived on their own. Particularly noteworthy is the genus *Pseudognaphalium*, previously unknown from Santa Barbara Island, but which is now represented by four species there (three native and one non-native). These results have implications both for management of invasive weeds, and in furthering our understanding of island biogeography. From the management standpoint, understanding where and how non-native plants arrive is an important step to limiting future, unwanted colonizers.

INTRODUCTION

The California Channel Islands have been the focus of a wide range of island biogeography studies, including analyses of 'turnover' rates and species richness patterns in birds (Diamond and Jones 1980; Lynch and Johnson 1974; Power 1976), species numbers and species—area relationships of amphibians and reptiles (Savage 1967; Wilcox 1980), species distribution and colonization of insects (Powell 1981, 1994), and biogeographic patterns of marine invertebrates and near-shore fish species (Pondella et al. 2005; Seapy and Littler 1980). In this way, studies on the Channel Islands have contributed to knowledge of regional faunal patterns, and also to more general questions of island colonization and community processes.

Compared to animal species, plants have been relatively neglected in studies of colonization on the California Channel Islands. Most studies of plants on the Channel Islands have focused on floristics and species diversity, including inter-island comparisons (e.g., Junak et al. 1995; Moody 2000; Oberbauer 2002; Raven 1967), patterns of endemism (Philbrick 1980), and effects of introduced herbivores such as sheep, goats, and pigs (e.g., Coblentz 1980; Hobbs 1980; Klinger et al. 1994; Peart et al. 1994). Floristic studies, which frequently make comparisons to other islands and nearby mainland floras, provide presumptive information on patterns of colonization, or at least successful establishment. Carlquist (1974) included San Clemente Island in the Channel Islands group in a comparison of different oceanic islands in relation to presumed colonization modes. However, there have been no previous studies that have directly examined current colonization patterns on any of the California Channel Islands.

Until recently, most studies of island colonization by plants have looked at devastated islands or newly formed islands. The most well-known of these include Krakatau, which was largely destroyed by volcanic eruption in 1883, and has slowly reformed. The island of Surtsey rose from the ocean off of Iceland in November 1963, and the arrival and spread of plant species on this new island have been followed since that time (e.g., Fridriksson 1987). However, colonization of barren, newly

formed or devastated islands is quite different from colonization of islands that have well-established plant communities. These latter islands have a more or less well-developed soil cover which is largely lacking on new islands, and potential colonizers face competition from established plant species. There have been very few studies (with the notable exception of Cody 2006) that have examined plant species colonization under such conditions. In this paper, we present another study of patterns of species arrival and colonization in an established island flora, on Santa Barbara Island, a small, comparatively isolated island in the California Channel Islands. We specifically describe and evaluate colonization rates and taxonomic patterns of both native and non-native vascular plants that have arrived on the island in the last 35 years.

STUDY AREA

Santa Barbara Island is located in the center of the Channel Islands group off the coast of southern California. It is a small island, measuring about 2.6 sq km in area, and is 62 km from the nearest point on the mainland coast. The nearest neighboring island is Santa Catalina, 38 km to the east. Santa Barbara Island is primarily volcanic, with thin layers of marine sediments. Topographically, the island has a series of low terraces, with small peaks at the north and south ends of the island. The highest point on the island is Signal Peak, at 193 m. Sheer cliffs bound much of the north, west, and part of the south sides of the island. Santa Barbara Island would have been completely submerged at high sea levels during the latter part of the Pleistocene, so the island's current biological history is presumed to be limited to within the last 100,000 years (Vedder and Howell 1980).

Coastal southern California has a Mediterranean climate, with mild winters and warm to hot summers, and most precipitation occurring as winter rains. On the offshore islands, particularly small islands like Santa Barbara, summer high temperatures and winter lows are strongly moderated by the surrounding ocean, so that seasonal temperature variation is comparatively low (Dunkle 1950; Philbrick 1972). On Santa Barbara Island, monthly average high temperatures range from 16°C in December and January to 23°C in August (Fellers and Drost 1991). Average annual precipitation has been reported from 22.7 cm (Fellers and Drost 1991) to about 30 cm (Dunkle 1950). Prevailing winds are from the west-northwest (Dunkle 1950; Philbrick 1972). Of possible significance to this study, however, are seasonal, strong east to northeast winds ("Santa Ana winds") that blow from the mainland out over the Southern California Bight at times during the fall and winter.

Like all of the Channel Islands, Santa Barbara Island has a long history of human impacts on the flora, ranging from introduced grazing animals to clearing and tilling for farming. Goats were recorded on the island as early as 1846, and farming families later brought sheep and other domestic animals (Philbrick 1972). European rabbits (*Oryctolagus cuniculus*) were introduced in the early 1900s, and at times increased to high numbers and caused severe declines in the native vegetation of the island (Sumner 1958, cited in Philbrick 1972). Larger grazing animals were taken off the island when grazing ceased in the late 1920s. European rabbits were successfully removed from the island by the National Park Service in 1981 (Junak et al. 1993; McChesney and Tershy 1998).

Visitation to the five islands that make up Channel Islands National Park is moderate, with approximately 30,000 visitors recorded in 2006. Santa Barbara Island receives fewer visitors than most of the other islands, because there is limited commercial transport to and from the island. In 2008, there were 332 visitors to the island via commercial tour boat (annual park visitor statistics, C. Leon., Channel Islands National Park, personal communication). Particularly during the summer, limited numbers of small private boats anchor at the island. Most of these come from the Los Angeles/ Long Beach harbors on the California mainland or from Catalina Island.

Several features of Santa Barbara Island make it a good study site to examine species arrival and colonization. It is small and topographically simple, and most of the island is easily surveyed. Steep cliffs on parts of the north and south sides are the only areas that cannot be accessed to survey on foot. The vascular flora is limited, numbering just over 130 taxa. Most of the vegetation on the island is low coastal scrub and annual grassland, and is relatively open and easy to traverse (Philbrick 1972). The

tallest (up to 2–3 m high) and densest vegetation is in some of the small canyons on the east side of the island. The flora of the island is also relatively well-studied. In addition to our own observations, we had the benefit of observations and collections by many National Park Service staff and visiting researchers over the course of this study.

Documented studies of the Santa Barbara Island flora began in the 1860s, though most work on the island dates from the early 1900s. At least 25 botanists, collectors, and observers have visited Santa Barbara Island (Junak et al. 1993). Particularly important studies include those of the Los Angeles County Museum Channel Islands Biological Survey, from 1939 through 1942. The botanical portion of this study was led by Meryl B. Dunkle, and culminated in the first comprehensive floristic list for Santa Barbara Island (Dunkle 1950). This was followed by studies conducted by staff of the Santa Barbara Botanic Garden, particularly Ralph Philbrick and associates. This work led to a detailed, revised flora for the island (Philbrick 1972), which provided the baseline for the study described here.

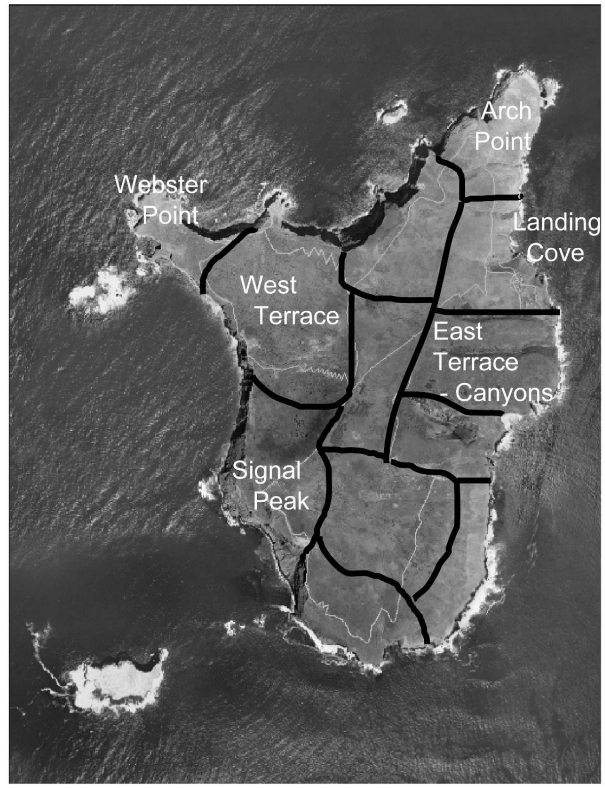

Figure 1. Santa Barbara Island, California, showing place names and the series of zones used in surveying for new vascular plant species.

METHODS

Our field surveys may be broken down into two general, complementary types. Junak conducted targeted searches around the island, looking for rare and unusual species. These observations were generally directed toward particular rare native species and habitats, but all species seen were noted. He also visited and read widely scattered permanent vegetation transects from 1978 through 2000 (e.g., Halvorson et al. 1988; Hochberg-Junak et al. 1983; Johnson and Rodriguez 2001; Corry and McEachern 2009). Drost added to these targeted searches with systematic surveys covering the entire island. For this purpose, the island was divided up into a number of zones (Fig. 1), and each zone was visited at repeated intervals (average of two to three visits per year). The zones were searched by walking through each defined area in a series of parallel lines spaced approximately 5 m apart, to ensure complete and uniform coverage of the entire area. New or unusual species were noted, and vouchers were collected or photographs taken. In the case of new native plants that were evidently rare (in some cases, single individuals), we limited voucher material to a small piece of the plant. In line with Channel Islands National Park management practice, we intentionally removed non-natives to the extent that we could.

We include as the time span of this study the period from Philbrick's (1972) flora up through 2007—a span of 35 years. Although we include observations from this entire time period and base our analyses on this interval, the most intensive fieldwork was during the period 1978 through 2000. Thus, field observations began while rabbits were still present on the island and continued after the last rabbit was removed in 1981. Junak and others from the Santa Barbara Botanic Garden and Santa Barbara Museum of Natural History conducted a detailed survey of the island's natural resources in 1978 and 1979, including mapping vegetation communities and the distribution of rare species (Hochberg et al. 1979; Hochberg-Junak et al. 1983). Junak spent 60 days on the island between June 1978 and April 2004, mostly during the spring months. During the 1980s, Drost spent over 900

days engaged in fieldwork on Santa Barbara Island, including observations on plants over the entire island. From 1981 through 1983, he averaged over 200 days per year on the island, in all months of the year. From 1984 through 1988, he spent from 30 to 80 days on Santa Barbara, from spring through early fall. Since that time, he has continued fieldwork on the island on an occasional basis, primarily in spring and early fall.

New species arrivals (and, in a few instances, changes in distribution and abundance of existing species) were determined with reference to the baseline provided in Philbrick (1972). We mapped the distribution of new species occurrences on the island, and noted habitat and location of new species in relation to trails, the National Park Service campground and visitor contact station, and other features and areas of human influence. Based on the total number of new species found, we calculated minimum arrival rates over the span of the study, for all species combined, and for native and non-native species separately. We specifically compare and contrast new native arrivals with new non-natives, with respect to taxonomic composition, spatial patterns on the island, and other aspects of species biology.

Throughout this paper, we refer to "native" species to mean plants that are native to the flora of California. In some cases, native mainland species may have arrived on the islands with human assistance, or may have spread on the mainland to an extent that they were then able to spread to offshore islands. For that reason, these species might be considered non-native in terms of the island flora. These distinctions are difficult to make with certainty, and we have not attempted to sort out such species for the purposes of this paper.

RESULTS

Between 1973 and 2007, we recorded a total of 32 species new to the flora of Santa Barbara Island (Table 1), including taxa documented by Junak et al. (1993) and taxa listed in Appendix A. These represented 11 plant families, two of which (Oleaceae and Tropaeolaceae, both non-native) were new to the flora of the island. One native species, the bush sunflower, *Encelia californica*, was probably missed in previous surveys as it was

Table 1. New vascular plant species found on Santa Barbara Island, California, during surveys from 1972 to 2007. Plant families are in alphabetical order, with dicots first and then monocots, and species are listed alphabetically within families. Non-natives species are noted by *.

Apiaceae	
	Apiastrum angustifolium
Asteraceae	
	Baccharis emoryi
	* *Conyza bonariensis*
	Conyza canadensis
	Conyza coulteri
	* *Cotula australis*
	Encelia californica
	Filago arizonica
	Filago californica
	* *Hedypnois cretica*
	Pseudognaphalium biolettii
	Pseudognaphalium californicum
	Pseudognaphalium canescens
	* *Pseudognaphalium luteoalbum*
Caryophyllaceae	
	* *Herniaria hirsuta ssp. cinerea*
	* *Polycarpon tetraphyllum*
	* *Spergularia bocconii*
	Spergularia salina
Chenopodiaceae	
	Monolepis nuttalliana
Fabaceae	
	* *Melilotus indicus*
Hydrophyllaceae	
	Eucrypta chrysanthemifolia
Oleaceae	
	* *Olea europaea*
Primulaceae	
	* *Anagallis arvensis*
Solanaceae	
	* *Lycopersicon esculentum*
	Nicotiana clevelandii
	Solanum douglasii
Tropaeolaceae	
	* *Tropaeolum majus*
Poaceae	
	* *Agrostis viridis*
	* *Cynodon dactylon*
	* *Lolium multiflorum*
	* *Poa annua*
	* *Schismus arabicus*

found on the remote, difficult-to-access cliffs on the south side of Signal Peak. We found a total of five large, spreading individuals of this shrub that appeared to be quite old, suggesting they were relict survivors from periods of intense grazing on the island. As far as we know, this steep cliff on the south side had not been previously accessed by other observers and collectors. Among the non-native species, the European olive (*Olea europaea*) represents a special case as well. It was obviously an intentionally planted individual, placed in lower Cave Canyon with the bottom half of a plastic milk jug still encasing the roots and soil (we removed this plant in its entirety). Neither *Encelia* nor *Olea* are included in the following analyses.

Not counting *Encelia* and *Olea*, the 30 new species include 14 natives and 16 non-natives. The native species represented six families, but were dominated by the family Asteraceae, with eight species in four genera (Table 2). The only other family with more than one native species was Solanaceae, with two taxa. Among non-native plants, the 16 species comprised 8 families. The largest of these was Poaceae, with five new species. This was followed by Asteraceae (four species) and Caryophyllaceae. Including both native and non-native species, the family-level taxonomic composition of new species was significantly different from the composition of the pre-existing flora of the island (Chi-square, p=0.044 for the six largest families). Some genera were represented by more than one new species for the island.

Table 2. Taxonomic breakdown of new native and non-native vascular plant species found on Santa Barbara Island, California, between 1972 and 2007.

Family	Native	Non-native
Apiaceae	1	--
Asteraceae	8	4
Caryophyllaceae	1	3
Chenopodiaceae	1	--
Fabaceae	--	1
Hydrophyllaceae	1	--
Oleaceae	--	1
Poaceae	--	5
Primulaceae	--	1
Solanaceae	2	1
Tropaeolaceae	--	1

Particularly noteworthy in this regard is the genus *Pseudognaphalium*, with four species (three native and one non-native; see Figs. 2a and 2b). Prior to this study, *Pseudognaphalium* had not been reported from Santa Barbara Island. *Conyza*, with three species (two native and one non-native) found since Philbrick's (1972) flora, is also a new genus for the island.

Many of the new species were first recorded as single individuals. Of the 30 total new species, 6 (20%) were single individuals. There was a trend for native species to be found as single plants, compared to non-natives, which were usually found as multiple individuals (Fisher Exact Test, p=0.072). Among native species, 5 of 14 new species (over 1/3 of the total) were single plants, including *Baccharis emoryi*, *Eucrypta chrysanthemifolia*, *Nicotiana clevelandii*, *Pseudognaphalium californicum*, and *Solanum douglasii*. Among non-natives, only *Tropaeolum majus* was represented by a solitary individual. In spite of intensive searches, we were unable to find additional individuals of any of these species in the year they were first found, and only one (*Pseudognaphalium californicum*) has persisted and spread on the island. Other species, such as *Conyza coulteri* (Fig. 2c), have been found as a very few individuals in different years.

Location and Fate of New Species

We noted clear differences between native and non-native species in terms of where new arrivals were first seen on Santa Barbara Island. Among non-natives, 9 of 16 were first found along the trail in Landing Cove canyon or in the adjacent campground/residence area—where people arrive at the island, unload supplies, and spend most of their time (Fig. 3). Four of the remaining seven species were found along the main foot trails that cross the island. Native species, on the other hand, were found scattered in a variety of habitats over most of the island (Fig. 4). Only two native species were associated with trails or other human facilities: *Monolepis nuttalliana*, first seen in disturbed soil along a trail above Landing Cove, and *Nicotiana clevelandii*, found along a trail at the south end of the island. Other native species were found in native shrub and shrub-grassland communities on the east terrace and around the canyons on the east side of the island, and in native shrub communities on the

Figure 2. New plant species documented on Santa Barbara Island, California. a) *Pseudognaphalium biolettii* is one of four species of *Pseudognaphalium* documented on the island (photo from north of head of Graveyard Canyon). b) *Pseudognaphalium californicum* was first recorded as a single individual, but has persisted (photo of first individual found, along south rim of Middle Canyon). c) *Conyza coulteri* has been found as a few widely scattered individuals, which may represent repeated arrivals at the island (photo from sea slope north of Landing Cove).

west slope and terrace. The north and west points of the island, with their shallow, rocky soil, were notable for their lack of new plant species.

Approximately half of the new plants we recorded on Santa Barbara Island have established at least a temporary foothold on the island (i.e., they have persisted for more than one generation). Among the native species, 7 of the 14 new species are known to be persisting (*Apiastrum angustifolium*, *Conyza canadensis*, *Filago californica*, *Monolepis nuttalliana*,

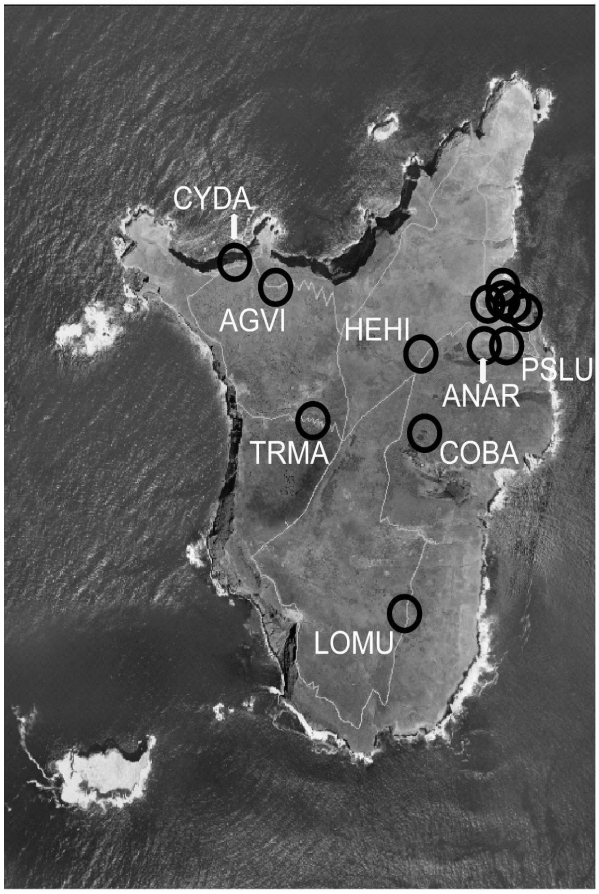

Figure 3. Locations where 16 new non-native plant species were first recorded on Santa Barbara Island, California, during surveys from 1973 through 2007. Eight species were found along the upper Landing Cove trail and north end of the visitor center building (cluster of overlapping circles towards upper right): *Cotula australis*, *Hedypnois cretica*, *Lycopersicon esculentum*, *Melilotus indicus*, *Poa annua*, *Polycarpon tetraphyllum*, *Schismus arabicus*, and *Spergularia bocconii*. Other abbreviations are: AGVI, *Agrostis viridis*; ANAR, *Anagallis arvensis*: COBA, *Conyza bonariensis*; CYDA, *Cynodon dactylon*; HEHI, *Herniaria hirsuta*; LOMU, *Lolium multiflorum*; PSLU, *Pseudognaphalium luteoalbum*; TRMA, *Tropaeolum majus*. The location of a single, intentionally planted individual of *Olea europaea* is not plotted.

Pseudognaphalium bicolor, *Pseudognaphalium californicum*, *Spergularia salina*). Among the non-natives, as many as 7 of 16 species have persisted over multiple years (*Conyza bonariensis*, *Cotula australis*, *Melilotus indicus*, *Poa annua*, *Pseudognaphalium luteoalbum*, *Schismus arabicus*, *Spergularia bocconii*). One questionable case is *Melilotus indicus*, which may have been introduced more than once. A small introduction was thought to have been eradicated after it was first found in 1982. This conspicuous species was not seen again for 12 years, when it was found along the main trail on the east terrace. In spite of their persistence, spread of most recently arrived non-native species has been limited so far. Only *Schismus arabicus* has spread widely, from near the north end of the island at Landing Cove to the south end of the island.

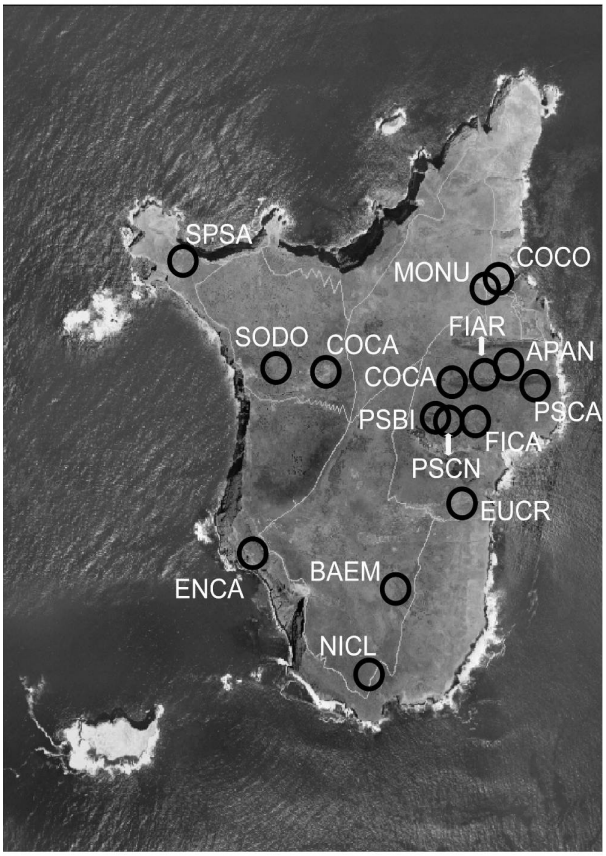

Figure 4. Locations where 15 new native plant species were first found on Santa Barbara Island, California, between 1973 and 2007. Abbreviations are: APAN, *Apiastrum angustifolium*; BAEM, *Baccharis emoryi*; COCA, *Conyza canadensis* (first found in two different locations); COCO, *Conyza coulteri*; ENCA, *Encelia californica*; EUCR, *Eucrypta chrysanthemifolia*; FIAR, *Filago arizonica*; FICA, *Filago californica*; MONU, *Monolepis nuttalliana*; NICL, *Nicotiana clevelandii*; PSBI, *Pseudognaphalium biolettii*; PSCA, *Pseudognaphalium californicum*; PSCN, *Pseudognaphalium canescens*; SODO, *Solanum douglasii*; SPSA, *Spergularia salina*.

DISCUSSION

We believe that survey coverage was intensive enough to detect nearly all new plant species that reached flowering stage on Santa Barbara Island. Coverage of the island was more limited between 1973 and 1977 and between 1994 and 1997, but between 1978 and 1993, and again between 1998 and 2000, one or both authors conducted extensive searches over the island at multiple times during the growing season. The number of species represented by single individuals, found only once and not seen in any other year, is one indication of the thoroughness of coverage. Likewise, almost all of the species that were recorded for the first time appeared to be new arrivals. Few of them are very small, cryptic, or otherwise likely to have been overlooked. Many of them, in fact, are comparatively large, conspicuous species that can be recognized over much of the growing season. With one exception, none of the new species were found in inaccessible or infrequently visited areas. *Encelia californica*, found on the steep sea cliffs on the south side of the island, is the only "new" species that was probably a relict survivor that had been overlooked by earlier observers.

There were clear taxonomic patterns among new species that arrived on the island. Among native plants, new arrivals were dominated by members of Asteraceae (Table 2). Among the non-natives, Asteraceae, Poaceae, and Caryophyllaceae contributed multiple species (Table 2). These taxonomic patterns reflect at least in part the dominant modes of dispersal of these plants. Carlquist (1974) included San Clemente Island in the southern California Channel Islands as part of an analysis of probable modes of dispersal contributing to island floras. His analysis is based on the native island flora, and a subjective evaluation of the means of dispersal by which propagules of each native species probably reached the island. Categorized in this way, the new native species that we documented on Santa Barbara Island present a distinctly different picture (Table 3). Particularly

Table 3. Comparison of probable dispersal modes for recent native plant arrivals on Santa Barbara Island, versus modes hypothesized for the flora of San Clemente Island (see Carlquist 1974).

	Santa Barbara		San Clemente
Mode	Number	Percent	Percent
A	8	57	18
BB	1	7	10
BI	1	7	40
BM	2	14	18
BV	2	14	5
DF	0	0	7
DR	0	0	1

Codes (after Carlquist 1974): A - aerial; BB - birds, seeds adhering with barbs, bristles, etc.; BI - birds, internal (fruits eaten by birds); BM - birds, seeds in mud on feet; BV - birds, seeds adhering by viscid coating; DF - drift / frequent (seeds capable of floating); DR - drift / rare (seeds arriving via rafting).

noteworthy in our results are the large number of wind-dispersed species (all of them Composites) on Santa Barbara Island, relative to the low percentage indicated for the San Clemente flora by Carlquist. Likewise, the largest component of the San Clemente flora is represented by plants with fruits that are eaten by birds and transported by them internally. The only new species on Santa Barbara Island that fits in this category is *Solanum douglasii*, which has a fleshy fruit eaten by birds.

Carlquist (1974) notes that presumed modes of transport are poorly studied and difficult to verify, so any such assessment has a measure of subjectivity. As a specific example among the new arrivals on Santa Barbara, the *Filago* species have some achenes with pappus and some achenes without (Hickman 1993). Even on the achenes with a pappus, however, the plumes are deciduous. Hence, the two *Filago* species may typically disperse to a greater extent by adhering to the feathers of ground birds, or by being transported in mud on the feet of birds.

The differences between our results and those of Carlquist (1974) are probably to be expected, however. Carlquist's analyses reflect the cumulative results of tens of thousands of years of colonization, competition, local extinction, and adaptation to the island environment. The shorter-term results for Santa Barbara Island represent species that disperse easily but may not become permanently established on the island. General studies of seed dispersal indicate that species with small seeds and high dispersal ability are good colonizers, but frequently do not persist for long in the face of competition (Howe and Smallwood 1982). The number of species that showed up briefly on Santa Barbara and then disappeared appears to reflect this pattern.

All of the new grass arrivals were non-native species. The lack of recent colonization by native grass species stands out (Table 2), given that grasses make up a high percentage of the native flora of the Channel Islands (e.g., 9.3% on Santa Barbara Island, Junak et al. 1993; 9.6% on San Nicolas Island, Junak 2008). Known or suspected modes of transport for the relatively large, heavy seeds of most grasses include rafting or water transport for strand grasses (e.g., Carlquist 1974) and transport of florets adhering to the feathers of birds or fur of mammals. However, because of the wholesale shift of grasslands in much of California to non-native annual species, the relative lack of native colonizers may be due to much-reduced mainland and near-island sources of propagules. On the other hand, many abundant introduced grasses have spiny awns and are effectively transported in the clothing and shoes of humans.

The Santa Barbara Island flora is surprisingly dynamic. Counting both native and non-native species, there have been approximately 0.85 new species per year over the span of this study. Broken down, this is 0.4 native and 0.45 non-native species per year. As already noted, many of these were represented by single individuals that did not persist. Any such waifs that were missed would increase the calculated arrival rates (on the other hand, if any "new" species were present but were simply missed by earlier surveys, the rates would be lower).

In comparison, Philbrick (1972) found a total of 20 new species since Dunkle's (1950) list. He considered that 5 of these, because they are inconspicuous or taxonomically difficult, may have been overlooked by earlier botanists. The remaining 15 species consisted of 8 natives and 7 non-natives. Over a 22-year period, this equates to 0.68 new species per year, or 0.36 native species, and 0.32 non-natives per year. By calculating annual rates, we do not mean to imply that arrival of new species on the island is expected to be constant. A variety of

factors such as rainfall, relative frequency of offshore winds from the mainland, and possibly reduced herbivory since the removal of European rabbits, may influence the probability of plant propagules reaching the island and successfully germinating and growing to maturity.

Considering other island systems, there are no perfect comparisons for our estimates of arrival rates on Santa Barbara Island. Differing island size, distance from mainland, latitude, composition of potential source floras, and successional state of the island flora all probably affect colonization rates. Nonetheless, comparisons with studies on other islands provide points of reference. The islands studied by Cody (2006) in Barkley Sound, British Columbia, have established floras, but they are generally much smaller (most much less than 1 km^2), and closer to mainland sources (< 1 km to about 8 km). Arrival rates on these islands ranged up to 2 species per year or more. The island of Surtsey off of Iceland is the closest to Santa Barbara in size (maximum of 2.7 sq. km, but now shrinking due to erosion) and distance from mainland (33 km), but it is a very new island (risen from the sea less than 35 years ago) and is at a much higher latitude. Early colonization rates were on the order of 1/year (Fridriksson 1987), but rates have increased to the order of 2–5 /year. Finally, the island of Nishino-shima is smaller (about 0.22 sq km) and much farther from the mainland (ca. 1000 km south of Japan). It has a measured colonization rate of 0.1/ year (Abe 2006).

Non-native Plants

Carlquist (1974) and Cody (2006) note that islands may be particularly prone to invasion by non-native plants, owing to their relatively depauperate floras. However, although theoretical studies all indicate that lower diversity should be associated with higher invasibility, and some experimental studies have also supported this, observational studies based on species lists suggest that areas with higher native diversity have higher numbers of non-native species (Levine and D'Antonio 1999). A more important and more consistent predictor of whether invaders establish on a site where they arrive may be disturbance—both natural and human-caused. Santa Barbara Island and the other Channel Islands have all experienced moderate to severe disturbance since being occupied by people. The fact that almost all non-native species have first been found along trails and around areas of human activity might also reflect continued disturbance of areas along trails and around buildings and other human-use facilities.

On the other hand, in a study of non-native plants on coral cays in the Great Barrier Reef region of Australia, Chaloupka and Domm (1986) found that the proportion of the flora represented by non-natives was correlated with frequency of human visitation. They further concluded that this was due to inadvertent human transport of non-native plant propagules ("anthropochory"), as opposed to habitat disturbance by humans that subsequently allowed colonization by wind or other mechanisms. New non-natives on Santa Barbara Island were not distributed widely on trails, cleared areas, and other human-disturbed habitats across the entire island. Rather, they were heavily concentrated in those areas of highest human traffic and initial entry onto the island, at Landing Cove and around the ranger station and campground. In agreement with Chaloupka and Domm (1986), this suggests that direct human transport of seeds and other propagules, rather than disturbance and opening of potential habitat, is mainly responsible for colonization by non-native species.

The locations where non-native plants were found (Fig. 3) also presents clear implications for management of invasive species. Nine of the new non-native species were found in the Landing Cove/ residence/campground area. Three of these were along the upper part of the Landing Cove trail, and three were found at the north end of the National Park Service visitor center, just beyond the top of the Landing Cove trail. Most of the remaining non-natives were found immediately along main visitor trails. Control of non-native plants is a high priority in protected areas. It is generally considered that the most important thing that can be done to stop invasion of exotic species is to detect them early, before they have a chance to spread widely and increase in numbers (e.g., Myers et al. 2000; Simberloff 1997). On the Channel Islands, regular surveys of the main visitor access areas (e.g., the Landing Cove area and main trails on Santa Barbara Island) would be a simple and cost-effective means of early detection of new non-natives. Islands have the obvious added advantage that it is easier to

control initial invasions and prevent reintroductions than it is in mainland settings (Brockie et al. 1988; Simberloff 2002).

Relationship to Vegetation Recovery

Introduced European rabbits formerly occurred on Santa Barbara Island, and prior to that, the island was farmed and grazed (Philbrick 1972; Junak et al. 1993). High rabbit numbers in the 1950s and a fire that burned most of the east side of the island in 1959 probably severely reduced and possibly eliminated some species. Paired photos taken in 1939–1940 and again in 1970 document persistent changes related to past disturbance of the island's vegetation, particularly in the reduction in cover and stature of native plant species (Philbrick 1972). Since the last rabbits were removed from the island in 1981, there have been conspicuous increases in the numbers and extent of some native shrubs on the island (Clark and Halvorson 1990; Corry and McEachern 2009).

Moody's (2000) analysis indicated that the number of native species on Santa Barbara Island was lower than expected, based on island size. It is possible that the combination of grazing, heavy browsing and digging by periodically very large populations of rabbits, and the 1959 fire reduced the number of plant species to a level from which the flora is still recovering. Clearly, new native plant species continue to arrive on the island. The effects of rabbits, past cultivation, and fire may also have influenced the observed colonization rate by opening up areas where colonizing species, especially invasive non-natives, could become established. Much of the east side of the island is still covered by a mix of exotic annual grassland and open badlands.

In contrast to some of the island endemic plants on Santa Barbara Island, which appear to have increased substantially since the removal of human disturbance (most recently, feral rabbits), the spread of newly established native colonizing species has been slow. *Pseudognaphalium californicum* and *P. biolettii* are still confined to scattered small areas in and around the canyons on the east side of the island, mostly in association with cactus patches. *Apiastrum angustifolium* is found on limited portions of the island's east terrace, in mixed grass–shrubland. Some other species noted by Philbrick (1972) also appear to be spreading very slowly. Philbrick found only a single individual of the large shrub *Baccharis pilularis* in his surveys. Eight individuals were noted by Junak in 1982 and 1983 (Junak et al. 1993), and a total of 11 were found in a reconnaissance of the entire island in 1998 (Drost, unpublished notes). Clearly the arrival and successful germination of a colonizing plant species on an island is just the first step in a long process.

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Appendix A. Additions to the known flora of Santa Barbara Island, California, since the publication of "A revised flora of Santa Barbara Island" (Junak et al. 1993). Included here are details of observations of previously unrecorded species, including herbarium specimen records, and descriptions of important changes in status or distribution of species on the island. Herbarium voucher specimens have been deposited at the Santa Barbara Botanic Garden (SBBG) unless otherwise noted.

Asteraceae

Filago arizonica A. Gray. Localized population on open south-facing slope along north rim of Middle Canyon, elevation ca. 160 ft, April 6, 2000, *Junak SB-179*; scattered on south-facing slope along north rim in central portion of Middle Canyon, elevation ca.170 ft, April 6, 2000, *Junak SB-183*.

Hedypnois cretica (L.) Dum.-Cours. Localized population of three individuals along trail at Landing Cove, just downhill from bench at switchback, elevation ca. 120 ft, June 7, 1999, *Junak SB-170*. This non-native taxon is also known from Santa Catalina Island and San Clemente islands. It has spread very rapidly, especially along roads, during the last decade on Santa Catalina Island.

Brassicaceae

Brassica nigra (L.) W.D.J. Koch. Along trail near NPS Ranger Station, 1995 or 1996, *Chaney s.n.* (SBBG 117128). Possible reintroduction to the island. Identification of this taxon is tentative as records are based on sterile specimens which may in fact be *Hirschfeldia incana* (L.) Lagr.Foss. Only known previous collection was by Dunkle in 1940. This conspicuous species was not seen during intensive surveys in 1981–1989, but was found again by NPS staff in 1995 or 1996. All individuals seen were removed.

Caryophyllaceae

Herniaria hirsuta L. var. *cinerea* (DC.) Loret & Barrandon. Rare in new gravel along trail to saddle, between Cave and Middle canyons, elevation ca. 420 ft, April 16, 1994, *Junak SB-109*. This non-native taxon has now been found on San Miguel, Santa Rosa, San Nicolas, Santa Catalina, and San Clemente islands as well (Junak 2008).

Polycarpon tetraphyllum (L.) L. Localized population on disturbed north-facing slope near top of Landing Cove trail, elevation ca. 130 ft, June 1, 1999, *Junak SB-146*. This non-native taxon has now been found on all of the California Channel Islands except San Nicolas and San Clemente.

Fabaceae

Melilotus indicus (L.) All. After its original discovery and targeted eradication efforts in the early 1980s, this conspicuous species was not seen again from 1985 through at least 1989, in spite of intensive surveys across the island. It may have been reintroduced with imported gravel and sand in 1994 and perhaps again in 1999. Scattered plants in new gravel along trail to saddle, between Cave and Middle canyons, elevation ca. 420 ft, April 16, 1994, *Junak SB-110*; two plants found on introduced sand at helicopter pad near ranger station above Landing Cove, elevation ca. 170 ft, June 7, 1999, *Junak SB-169*.

Oleaceae

Olea europaea L. At base of north-facing slope in lower Cave Canyon, near mouth; in milk jug 'pot' buried in ground, among Coreopsis. This obviously intentionally planted individual was removed in its entirety. A specimen was not kept.

Pages 229–244 in Damiani, C.C. and D.K. Garcelon (eds.). 2009. Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.

A SPATIAL DATABASE OF SANTA CRUZ ISLAND VEGETATION

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Abstract—In 2006, The Nature Conservancy (TNC) contracted with Aerial Information Systems (AIS) to create a spatial database of vegetation on Santa Cruz Island, a 243 km^2 island jointly owned and managed by TNC and the National Park Service (NPS). AIS and TNC developed appropriate vegetation categories down to the alliance level, based on plot and transect data provided by USGS-Biological Resources Discipline, NPS, and TNC; *The Manual of California Vegetation*; and site visits conducted during the course of the project. A minimum mapping unit of 0.5 ha was established for the delineation of a visible alliance or mapping unit. AIS used 1:12,000 natural color aerial photographs from 2005 for the manual delineation of polygons. The delineation protocols established specific methods and criteria for each alliance or mapping unit and documented them for future updates, creating the foundation for tracking changes over time using sequential mapping techniques. The resulting vegetation database is discussed in relation to the changes that have occurred on the island over the last 20 years, specifically the removal of feral ungulates on the island, and is compared to earlier vegetation mapping efforts. The specific attributes developed for the database, particularly the cover measure and location of fennel, enable the exploration of more sophisticated and robust research questions.

INTRODUCTION

Mapping and tracking changes in vegetation patterns are essential to the management and long-term protection of landscape-scale biodiversity and ecological processes. The Nature Conservancy (TNC), which owns and manages 76% of Santa Cruz Island (SCI), was particularly interested in documenting changes in vegetation as a result of feral ungulate removal programs over the last 25 years. To that end, TNC contracted Aerial Information Systems (AIS) in 2005 to create an island-wide spatial vegetation database at a high spatial and categorical resolution and to document the methods sufficiently to allow for future updates. This paper describes the methodology used to create this database, discusses the information collected on vegetation types and cover, and compares the new database to earlier mapping efforts of the island.

Sheep, pigs, and cattle were introduced to SCI in the mid-1850s (Hochberg et al. 1980; Junak et al. 1995), marking the beginning of severe ecological degradation of the island (NPS 2002). All three ungulates ate native plant species, including some that were unique to the island (Hochberg et al. 1980). After acquiring an interest in the island in 1978, TNC began a program to eradicate sheep, and later cattle and pigs, from their portion of the island. Beginning in the 1990s, the National Park Service (NPS) conducted a similar eradication of feral animals from their portion. Over 46,000 sheep were removed from SCI between 1981 and 2001 (Morrison 2008), and between 1988 and 1989 nearly 2000 head of cattle were rounded up and shipped to the mainland (P. Schuyler, personal communication) Finally, over 5000 feral pigs were eradicated from the island between 2005 and 2007 (Morrison et al. 2007).

The removal of non-native grazers was expected to have significant ecological consequences, especially on vegetation. Photomonitoring conducted between 1980 and 2006 has already shown increases in native plant cover at several sites around the island (P. Schuyler, personal communication). To better understand these changes, we embarked on a program to develop a cost-effective, large-scale vegetation monitoring methodology to provide information supporting long-term adaptive management of the island's resources. Previous vegetation mapping

efforts of the island (Minnich 1980; Jones et al. 1993) provide a general overview of the vegetation communities. However, they do not have enough accuracy or precision to describe the island's subtle and complex community compositions. The methodologies employed in these mapping efforts are also not documented in enough detail to sufficiently replicate them, and therefore have limited value for supporting current and future management decisions. In this paper, we describe the development of a vegetation database at high spatial resolution that will facilitate the monitoring, management, and recovery of distinct plant communities.

STUDY AREA

SCI is situated 55 km west of Los Angeles and 40 km south of Santa Barbara, and is the largest of the California Channel Islands. The island trends east to west, and has roughly 124 km of coastline. The 249 km^2 island includes two mountain ranges flanking a central valley, a long east-west isthmus, and an eastern end fairly isolated by a high and steep ridge. It sustains more than 625 plant species (Junak et al. 1995), 198 bird species (Jones et al. 1998), and 12 species of native reptiles, amphibians, and terrestrial mammals (Laughrin 1980).

In 1978, a 90% interest in SCI was purchased by TNC, and outright ownership was gained in 1987. TNC transferred 8,500 acres (14% of the island) to the National Park Service (NPS) in 2000, adding to the 10% of the island that had been designated a National Park in 1980. The island is managed cooperatively by both land owners.

METHODS

Based on the desired level of spatial and categorical specificity, and the amount of funding available, aerial photo interpretation was selected to create the database. Knapp (2005) described the following reasons for selecting aerial photo interpretation versus remote sensing for the vegetation mapping of another Channel Island, Santa Catalina Island: 1) aerial photography provides higher resolution than satellite imagery; 2) satellite imagery requires extensive ancillary data and additional labor to classify plant communities; and 3) some plant communities are too spectrally similar to be differentiated in satellite imagery. Knapp also suggested that mapping at very high resolution provided reduction of intra-polygon heterogeneity, as well as capturing of localized vegetation change. IK Curtis Inc. (Burbank, CA) was contracted to acquire and print 156 1:12,000 stereo pair, true color aerial photographs of the island. The flights to acquire these images were conducted in November 2005.

To generate the vegetation map, photo interpreters reviewed aerial photographs to identify photo signatures—unique combinations of color, texture, tone, and pattern associated with each land cover feature. By observing the context and extent of the photo signatures associated with specific vegetation types, the photo interpreter is able to identify and delineate boundaries between plant communities, resulting in the creation of mapping units or polygons with distinctive photo signatures. These photo signatures are then linked to vegetation attributes (e.g., type, cover, and the fennel mapping unit) observed in the field using a classification system and photo interpretation key. In the following sections, we describe the methods for field data collection and development of the classification system, photo interpretation, data conversion of the final map layers, and accuracy assessment.

Field Data Collection and Classification System

We selected a floristic-level classification system based on Sawyer and Keeler-Wolf's (1995) and the newly revised alliance-based classification system for California (Sawyer et al. 2009). This was determined suitable for the management needs of island projects based on the system's ability to capture rare plant assemblages, its ability to be combined into coarser levels of classification (Knapp 2005), and its consistency with the National Vegetation Classification System (Grossman et al. 1998; Jennings et al. 2003). This system is being adopted by the Federal Geographic Data Committee (FGDC 2008) in the draft National Vegetation Classification Standard (Version 2.0), and is becoming more widespread in vegetation mapping projects in California (D. Johnson, personal communication). We considered it to be important to add to the developing statewide body of

knowledge of vegetation, while maintaining the ability to compare with earlier vegetation maps and vegetation databases of other Channel Islands. It is important to note, however, that the classification used for this project was derived from field sampling and analysis, and then expanded based on expert opinion, and thus did not rest completely upon the field-based classification process used in other recent studies. Therefore, although the shape and size of each mapped polygon are likely to remain constant, their nomenclature may formally change in the future if further field classification and data analysis are done.

The classification system for SCI is arranged hierarchically from class to formation, to mapping unit or alliance, and finally sub-alliance or potential association, with class being the most inclusive category and sub-alliance being the least inclusive (Table 1). Primary sources of data used to determine the floristic composition of each mapped polygon and develop the classification system were data from a series of 362 relevé plots, field reconnaissance, and *A Flora of Santa Cruz Island* (Junak et al. 1995).

Relevé Plots: The relevé plots are a series of 362 locations spread non-systematically across the island, developed and maintained by the USGS and the NPS. At each point a visual survey is undertaken to record a variety of aspects of the plot location, including the physical characteristics of slope and aspect, soil depth, and elevation; community type or types, size, and distance to nearest adjacent stand; animal disturbance; substrate; species information including coverage and phenology, stratum, and tree diameters; and associated species. Each plot is 40 m by 10 m, with the long axis parallel to the major landscape slope. The community types are derived from those detailed in *A Flora of Santa Cruz Island* (Junak et al. 1995).

Field Reconnaissance: Two field reconnaissance trips were made to SCI to identify the floristic composition of vegetation types to be used in the classification system. The first trip was conducted in July 2006 to the west side and the isthmus (TNC side of the island), and the second was made in August 2006 to the east side of the island (NPS side). Field reconnaissance was performed by AIS photo interpreters and the senior ecologist from California Department of Fish and Game's Vegetation Classification and Mapping Program (Todd Keeler-Wolf), who served as a reconnaissance advisor and expert on the classification of California vegetation types. TNC ecologists also accompanied the reconnaissance team on field visits. The field reconnaissance visits served two major functions. First, they allowed the photo interpreter to key the signature on the aerial photos to the vegetation on the ground at each site. Second, they allowed the photo interpreter to become familiar with the flora, vegetation communities, and local ecology that occur in the study area. Understanding the relationship between

Table 1. Hierarchy of vegetation classification used to map Santa Cruz Island in 2006 compared to other established vegetation classification hierarchies.

Sawyer et al. (2009) classification	U.S. National Vegetation Classification	AIS (2007) level of vegetation classification	Example (Code – Type)
Formation subclass	Class	Class	1000 – Forest
Formation	Subclass		
Division	Group		
Macrogroup	Subgroup		
Group	Formation	Formation	1200 - Temperate Needleleaf Evergreen Forests
Alliance	Alliance	Mapping unit or alliance	1210 – Bishop Pine Alliance
Association	Association	Sub-alliance or potential association	1213 – Bishop Pine / Island Scrub Oak – Island Manzanita

the vegetation units and the environmental context in which they appear is useful in the interpretation process, and familiarity with regional differences aids interpretation by establishing a context for a specific area.

Prior to the field reconnaissance trip, each aerial photo was reviewed under a stereoscope for representative signatures of different vegetation types; geographic variables (% slope, aspect, shape of the slope, elevation); and other abiotic variables noted on the photography. Field check sites and associated notations were annotated directly onto a photo field acetate overlay, thereby correlating the field site to a specific location and photo signature. Multiple sites were chosen to provide alternatives if one or more sites proved inaccessible. Additional field sites included areas encountered in transit between initially selected sites, areas of noteworthy or unusual significance, and other vegetation types the photo interpreter or field ecologist deemed important. Field routes were then planned to accommodate a variety of factors including: maximizing the number of vegetation communities and elevation zones visited, responding to any recommendations of project staff, addressing time constraint considerations, and accessibility.

A total of 350 ground control points were taken in the field with a GPS unit. Distance and direction data measured by laser range-finder and compass in the field were then used to correct these locations. The environmental setting, dominant vegetation, and potential alliance were described for each ground control point. Color ground photos were taken with a digital camera at selected locations, to be compared later to the aerial photographs and the field site notes. Using information derived from the field reconnaissance and any existing field plot data, Keeler-Wolf developed a preliminary mapping classification and photo interpretation signature key based on the rules of the National Vegetation Classification system and existing information from other parts of California. Photo interpreters used *A Flora of Santa Cruz Island* (Junak et al. 1995) to aid in the development of the preliminary mapping classification. In addition, the vegetation map created by Richard Minnich in 1980 (*Vegetation of Santa Cruz Island*) was used to help photo interpreters further correlate aerial photo signature with previously mapped vegetation stands, with the understanding that the 1980 mapping product was created under a different set of criteria over 25 years ago. This system was revised based on realistic concerns of size and discernability of the different vegetation types. Not all of the categories could be mapped from the aerial photography. Mapping of these categories therefore relied on plot data, field visits, personal expertise, and other ancillary information, including IKONOS multi-band satellite imagery from April 2005.

Preliminary Photo Interpretation

Photo interpretation (PI) is the process of identifying polygons based on their photo signature. Photo interpretations for the SCI map were done using aerial photography at a scale of 1:12,000 (1” = 1000 feet). Photo interpreters used 3X ocular lenses to enhance line detail to a scale of approximately 1:3000. Viewing the final rectified linework over imagery at scales larger than 1:3000 may show spatial errors, which are beyond the resolution of the input scale at which the interpretation was originally performed. Each aerial photo was prepared with a 9” x 9” frosted Mylar overlay for the photo signature delineations. Study area boundaries were drafted onto each photo overlay, defining the area within the photograph to be interpreted. The study area boundaries were edge matched to adjacent photos to ensure complete coverage. Data from additional collateral sources (existing vegetation maps, supplemental imagery, soil data, plot data, etc.) were added to the overlay in order to document all locations and information within the study area on an aerial photograph.

Using a mirror stereoscope, with a 3X ocular lens, photo signature units were delineated onto the overlay. These initial photo delineations were based on a number of signature characteristics including color, tone, texture, relative height, and cover. Environmental factors such as elevation, slope, and aspect were also considered in the photo interpretation decision-making process. Attribute codes were assigned to each polygon and annotated onto the overlay. The vegetation polygons and codes were edge matched to the adjoining photo overlays. Areas of land use were also mapped during the mapping of the vegetation units. In addition to the criteria for defining each community or alliance, the interpretation was conducted in accordance with the preliminary mapping classification created as a result of the field

reconnaissance trips. Any questionable photo signatures encountered during this phase of the mapping effort were sent to the TNC field ecologist (Coleen Cory). This required her to either use her existing knowledge of the area or go out into the field to the site in question to get an answer.

Attributes assigned to each polygon included a vegetation classification type, a fennel category, and a cover rating. Specific management needs related to the concern over the status and trends of problematic pest plants required the inclusion of a primary category for fennel (*Foeniculum vulgare*), along with an attribute modifier that described a categorical estimate of fennel cover for areas that contained fennel. If fennel was interpreted as the dominant species for a polygon, that polygon was assigned the specific fennel category. Other areas that contained fennel were assigned a value (#) corresponding to <5% (1), 5% to 10 (2), or > 10 (3).

Vegetative cover is a quantitative estimate of plant cover derived from viewing the aerial photography in stereo magnification. Each polygon had a cover rating assigned to three different categories: conifer, hardwood, and shrub. The three cover estimates assist in describing the vegetation characteristics of each polygon. Photo interpreters used six categories to define vegetative cover: 1 = Greater than 60%; 2 = 40%–60%; 3 = 25%–40%; 4 = 10%–25%; 5 = 2%–10 %; 9 = Not applicable. Photo interpreters can only quantify the vegetation that is visible on the aerial photography and therefore total vegetative cover may differ from assessments done on the ground by field crews. Using aerial photography at scales smaller than about 1:12,000, photo interpreters generally cannot see the amount of vegetation that is obscured by a higher canopy, regardless of its life form. Understory vegetation that is not visible on the aerial photograph cannot be quantified when assigning the total cover of vegetation for that polygon. Assigning cover values to the polygons required AIS to develop a series of rules for assigning these values:

1) To determine vegetative cover, assign percentages to the different life forms visible on the aerial photo, including non-vegetated areas. The total percent cover of conifer trees, hardwood trees, shrubs, herbaceous, and non-vegetated must add up to 100%. The cover percentages are then converted into the six cover categories described above.

2) Do not code non-vegetated areas unless they meet the 0.5 ha minimum mapping resolution and can be mapped as a stand-alone polygon. Otherwise, it was assumed that all vegetation polygons contain some non-vegetated areas.

3) Consider the coverage pattern of the life form before assigning a cover code to the polygon. Estimating cover is more straightforward when plants occupying the same strata are evenly distributed throughout the polygon. However, when polygons contain populations of plants that are clumped or occur only in portions of the polygon, the area that is not occupied by plant cover is considered when determining total cover. To ensure consistency, count the plants in polygons with clumped and unevenly distributed vegetation and then compare them to similar sized polygons with an even distribution of plant cover.

4) Use vegetation stature and the scale of the aerial photography to determine the visibility of individual plants. With larger scale photography, trees and shrubs were usually visible as individuals. Grasses were rarely seen as individual plants, regardless of the scale of the photography.

5) In the case of trees and shrubs, the percent cover at a cover break was adjusted downward. If the percent cover was at about 25%, the polygon was assigned a cover category of sparse (10%–25%) instead of dispersed (25%–40%).

6) Dry grasses tend to be less dense than they appear on the aerial photography. To more accurately depict the cover, the percent cover for dry grasses was adjusted downward. If the percent cover fell at the lower end of a cover class, the polygon was assigned the next cover class down. For example, if the percent cover was 25%, the polygon was assigned a cover category of sparse (10%–25%) instead of dispersed (25%–40%).

7) The date that the aerial photography is flown also influences the cover assigned to vegetation types, especially for herbaceous dominated vegetation types. Subsequent field verification and accuracy assessments must take into consideration the following factors that can cause apparent discrepancies between the cover evident on the photo and those visible in the field:

a) Seasonality—The cover of most herbaceous plants is variable due to their annual growth cycle. Depending on the season the aerial photography was taken, a mapped polygon

could show a different cover on the aerial photographs than is observed during an on-site visit at a different time of the year. Another effect of seasonality is "leaf on/off" conditions. Photos of forest or woodland areas with "leaf on" conditions obscure the understory. Photos of leaf off conditions would allow photo interpretation of the understory, but make it difficult to identify the overstory species since there is no foliage present.

b) Annual variability—The environmental conditions at the time of the photography (wet vs. drought years, flooding, etc.) may affect the cover seen during the on-site field visits.

The size of a minimum mapping unit was 0.5 ha (5000 square m). This minimum mapping unit represented a compromise between the desire to have as much spatial and categorical detail as possible, and the reality of available funding. Exceptions to this minimum mapping unit were made for unique vegetations types and features that are often smaller than 0.5 ha in the landscape (Table 2). Distinct vegetation polygons smaller than 0.5 ha that were surrounded by spatially larger vegetation types were incorporated into the surrounding dominant vegetation type. The delineated vegetation boundaries represent the photo interpreter's estimate at defining the modal break point between two communities, whether at a detailed association level of mapping or at a more general habitat level (AIS 2007).

AIS created detailed documentation that describes how each category was delineated. These descriptions include mapping descriptions, environmental setting, distribution, and photo interpretation signature—mapping characteristics. This documentation is too large to include in this paper, but can be acquired from: http://www.tnccalifornia.org/gis/.

Data Conversion

Data automation was conducted using Mono Digitizing Stereo Digitizing (MDSD) software. Control points were identified both on the IKONOS imagery and the aerial photography and were input into an ARC/INFO point coverage. The MDSD software captured the vegetation linework, automatically georeferenced the data into real world coordinates using the control points generated in the previous step, and converted the linework into an

Table 2. Vegetation features mapped at scale less than 0.5 ha.

Type	# of polygons	Min. polygon size (ha)	Max. polygon size (ha)	Avg. polygon size (ha)	Total area (ha)
Australian Saltbush Mapping Unit	52	0.13	30.34	2.16	112.56
Big Leaf Maple Alliance	4	0.16	0.61	0.44	1.77
Bracken Fern Alliance	3	0.11	3.44	1.41	4.24
Coastal Salt Pan Mapping Unit	4	0.25	0.65	0.42	1.66
Fremont Cottonwood – Black Cottonwood Superalliance	32	0.06	2.07	0.53	16.86
Giant Wildrye – Creeping Wildrye Superalliance	14	0.17	1.55	0.61	8.56
Harding grass	14	0.06	12.52	2.33	32.61
Ironwood Alliance	483	0.03	3.73	0.37	178.94
Saltgrass Alliance	39	0.05	14.07	1.52	59.25
Sea Blite San Miguel Island Locoweed	33	0.19	3.88	0.86	28.33
Silver Beachbur – Beach Sand – Verbena Alliance	23	0.07	3.02	0.89	20.45

ARC/INFO coverage. The coverage was checked for open polygons, data registration, and any spatial edge match problems between photos. Spatial refinement was performed in ARCEDIT sessions using various user-defined tools. Lines depicting boundaries representing minimal ecotones (for example—land use interface, water bodies, life-form interface) were refined.

The vegetation mapping type, conifer cover, hardwood cover, shrub cover, and fennel component modifier codes were input for each polygon based on those created by the photo interpreter during the mapping phase. Automated quality control measures that AIS created were run to check for code validity.

A hard copy edit plot of the converted spatial data was produced and compared to the aerial photo overlays. Each plot was checked for cartographic quality of the arcs defining the polygon features and the accuracy of the label assignments. Line and code corrections were noted directly on the edit plot. All edit plots were edge matched to verify line and code accuracy across the entire project area. Processors conducted interactive ARCEDIT sessions to make the necessary corrections to the coverages. The final vegetation layer was examined by the senior photo interpreter. Final checks were conducted to test for invalid codes, duplicate labels, missing or extra lines, edge match problems, verification of the registration of linework to the IKONOS base imagery, and review of the distribution of species mapped within the study area.

Accuracy Assessment

Upon completion of the preliminary photo interpretation, the senior photo interpreter reviewed each photo for polygon delineation, PI signature code, cover codes, and fennel modifier accuracy. Each photo overlay was checked for completeness, consistency, and adherence to the mapping criteria and guidelines established by AIS. A rigorous quality control/ field verification effort was undertaken in order to assure consistency throughout the mapping product and to ensure photo signatures were accurately depicting what was noted on the ground. This effort was accomplished by creating hard-copy plots at a scale of 1:8400. These depicted the polygon data over the CIR imagery, with a 1000 m UTM grid draped over the entire map. All relevant data including the floristic code, density, and other modifiers were labeled in the polygon. Using a GPS along with a rangefinder, compass, and the hard copy plots, photo interpreters accompanied the island ecologist, Coleen Cory, on a 1-week effort to locate and check over 300 polygons within a ½ mile buffer from most of the travelable roads on the island. This represented slightly fewer than 3% of the total polygons mapped. Once this effort was completed, photo interpreters made corrections to polygons that were noted in the field verification effort. In addition, any incorrect trends between what was mapped to the aerial photo signature and what was actually found on the ground were refined and corrections were extrapolated onto the remainder of the map. Due to financial and time related constraints, AIS was not contracted by TNC to perform a formal accuracy assessment on the final database.

RESULTS

The resulting database contains 10,652 polygons ranging in size from 0.03 ha to 624.19 ha, with a mean of 2.33 ha. The final vegetation map can be downloaded from TNC's Web site: www.tnccalifornia.org/conservation/sciveg.html. The classification system begins with five classes: Forest, Woodlands, Shrublands, Herbaceous, and Land Use/Sparsely or un-vegetated. Shrublands are the dominant class, covering roughly 70% of the island (see Appendix). Herbaceous vegetation is the second largest class, at 21.2%. Forest, consisting predominantly of Bishop Pine forest, covers 3.8%. The Woodlands and Land Use classes make up the remainder of the island, covering 2.8% and 2.4%, respectively.

The five classes are further broken down into 17 formations. These formations were further broken out into mapping units or alliances, and then even further into sub-alliances or potential associations, where possible (see Appendix). For example, the Shrublands class contains four formations: Temperate Broadleaf Sclerophyll Evergreen Shrublands (Chaparral); Temperate Microphyllous Evergreen Shrublands; Temperate Xeric Mixed Drought-Deciduous Shrublands; and Temporarily Flooded Cold Season Deciduous Shrublands. Nested within the Temperate Broadleaf Sclerophyll Evergreen Shrublands (Chaparral) formation is the

Table 3. Summary of cover estimates.

Cover category*	Conifer (ha)	% of island	Hardwood (ha)	% of island	Shrub (ha)	% of island
1	18.6	0.1%	244.9	1.0%	3398.4	13.6%
2	153.3	0.6%	301.6	1.2%	2101.1	8.4%
3	160.7	0.6%	222.0	0.9%	3109.4	12.5%
4	331.3	1.3%	193.1	0.8%	7158.1	28.7%
5	516.2	2.1%	1904.2	7.6%	6511.1	26.1%
Totals	1180.1	4.7%	2865.8	11.5%	22,278.1	89.5%

*Cover categories: 1 = >60%; 2 = 40%–60%; 3 = 25%–40%; 4 = 10%–25%; 5 = 2%–10%.

Island Scrub Oak alliance. That alliance comprises 26.2% of the area mapped in its class (Shrublands), and 89.2% of the area mapped in its formation. Nested within the Island Scrub Oak alliance are six sub-alliances, the largest of which is Island Scrub Oak–Island Ceanothus, which accounts for 37% of the alliance, 33% of the formation, 9.7% of the class, and 6.8% of the island. The 720.3 ha assigned to the Island Scrub Oak alliance could not be further classified into one of the six sub-alliance and represents 15.8% of that group.

Cover

Assigning one of five cover categories for conifer, hardwood, and shrub cover to each vegetation polygon yields a multitude of combinations between vegetation type and woody species cover. There are 125 possible unique descriptors of woody species cover that could be assigned to each of the 10.652 delineated polygons and 216 combinations if a zero value is one of the cover values.

Conifers, hardwoods, and/or shrubs occurred in sufficient cover over nearly 90% of the island to allow a cover estimate to be assigned to at least one of these woody plant groups (Table 3). The remainder of the island did not have sufficient woody cover to be assigned cover estimates for conifers, hardwoods, or shrubs. Over half of the island was mapped as having a shrub cover <25%. The re-establishment of shrubs into grasslands or barren areas post-grazing may account for these low cover estimates. The cover measures for conifers may also describe regeneration patterns. Over 70% of areas with conifers exhibit conifer cover <25%. Cover values for hardwoods are even lower. Two-thirds of areas with hardwoods show cover <10%.

Fennel

Polygons dominated by fennel account for roughly 1% of the island. Polygons that were given a fennel modifier, indicating some amount of fennel was present, represent another 6% of the island. Nearly 40% of this latter category consists of fennel occurring in the California Annual Grasslands alliance. Another 20% consists of fennel occurring in the Coyote Brush alliance. In total, 3% of the island has vegetation where fennel comprises >10% of the vegetation polygon (Table 4).

Table 4. Summary of area mapped with fennel modifier.

Fennel modifier*	Ha	% of island
4301 Fennel dominant	244.9	1.0%
3 – Severe**	489.1	2.0%
2 – Moderate	335.4	1.3%
1 – Minimal	679.7	2.7%

* 1 = Minimal: Generally less than 5% cover of fennel in the polygon. Photo interpreters may or may not be able to detect these small amounts, and ground based information is often necessary in assigning a fennel modifier of 1.

2 = Moderate: Approximately 5%–10% cover of fennel over most of the polygon. Polygons with this cover class are visible on the aerial photography.

3 = Severe: Over 10% cover of fennel is in the polygon. Fennel is often a co-dominant to other herbaceous vegetation.

** In this table Fennel modifier "severe" does not include polygons in the 4301 mapping unit.

Table 5. Comparison of vegetation classification categories used in previous vegetation mapping of Santa Cruz Island.

Minnich 1980	Jones et al. 1993
Based on 1970 photos	Based on 1985 photos
Physiognomic type	Vegetation class
Grasses	Grasses
Coastal Sage Scrub	Coastal Sage Scrub
Chaparral	Chaparral
Woodlands	Island Oaks*
	Oaks
	Island Ironwoods
Conifer Forest	Pines
Riparian	Riparian
Woody Exotics	Woody Exotics
Barren	Barren

* Island Oaks refers only to *Quercus tomentella*. All other oaks are included in "Oaks" category.

Accuracy Assessment

While no formal accuracy assessment was performed, the field verification process found a few labeling discrepancies that were subsequently corrected. Of the roughly 300 polygons checked for accuracy, fewer than 10 polygons required changes to their attributes.

DISCUSSION

The spatial database created as a result of this mapping project represents the vegetation conditions on SCI at the end of 2005. As management of island resources continues, we will want to track changes in vegetation that may result from our management. This is best done by conducting an update to the spatial vegetation database in the future. The decision rules described, implemented, and documented by AIS will allow us to reproduce methodology so that future iterations of the database will be both spatially and categorically comparable. Furthermore, the database structure will allow updates and future mapping data to be seamlessly integrated with existing data. In a similar fashion, if other California Channel Islands were mapped using these same protocols, data could be easily compared across islands.

Minnich (1980) created a vegetation map for SCI using 1:22,000 scale color infrared aerial photography dating from 1970. No *a priori* classification system was used. Vegetation was instead grouped by floristic and physiognomic characteristics and assigned to one of eight physiognomic types: Grassland, Coastal Sage Scrub, Chaparral, Woodlands, Conifer Forest, Riparian, Woody Exotics, and Barren (Table 5). These types were further subdivided into one of 36 vegetation sets based on the dominant species as discerned from the photos.

Jones et al. (1993) used 1:24,000 scale aerial photography dating from 1985 to create an SCI spatial vegetation database based on a classification scheme devised by Philbrick and Haller (1977). Island vegetation was assigned to 1 of 11 vegetation classes based on tone, texture, and context of vegetation observed in aerial photos (Table 6).

Table 6. Changes in vegetation cover between 1985 and 2005 on Santa Cruz Island.

Vegetation type (from Jones et al. 1993)	Hectares (1985)	Hectares (2005)
Grasses	16,578.8	5037.5
Coastal Sage Scrub	809.7	11,921.7
Chaparral	3585.8	5153.2
Oaks*	1031.0	666.2
Island Ironwoods	103.6	179.1
Pines	292.1	664.0
Riparian	463.8	373.5
Woody Exotics	27.1	33.6
Barren	1665.6	569.6

*The "Oaks" category from 1985 includes several species of oaks (but not island oaks) and thus represents more acreage than the 2005 data, which distinguishes among these oak species and assigns them to different and finer scale mapping units.

NPS (2004) created a vegetation database, using 2-ft digital aerial photography, that classified the vegetation at the formation or sub-formation level where possible. These types included medium tall grassland (35%), mainly deciduous shrubland (25.4%), mainly evergreen shrubland (22.6%), mainly evergreen woodland (9.5%), forb-dominated vegetation (5.4%), mainly evergreen forest (0.25%), mainly deciduous woodland (0.6%), human use (0.1%), and mainly deciduous forest (> 0.1%).

Despite the differing methodology and vegetation groupings, we attempted to conduct a comparison between the 1985 (Jones et al. 1993) mapping data and our 2005 data. We constructed a cross-walk table that assigned each of our 2005 vegetation categories to one of the more inclusive categories from 1985. We assigned these categories based on physiognomic characteristics, species composition, and spatial distribution. Bare ground decreased dramatically during the intervening 20 years while at the same time all types of vegetation expanded across the island (Fig. 1; Table 6). The increase in vegetative cover corresponds to the time period during which more than 46,000 feral sheep and the remaining 2000 head of cattle were removed from the island.

Subsequent mapping can be used to track additional changes that are likely to occur as a result of removing more than 5000 feral pigs from the island between 2005 and 2007. Pigs demonstrated a food preference for certain plants, both native (oaks and bulb plants) and non-native fennel (NPS 2002). Their absence from the island may be reflected in shifting vegetation patterns that can be detected through fine-scale vegetation mapping.

Fennel is a perennial herb native to the Mediterranean basin. It was introduced to SCI

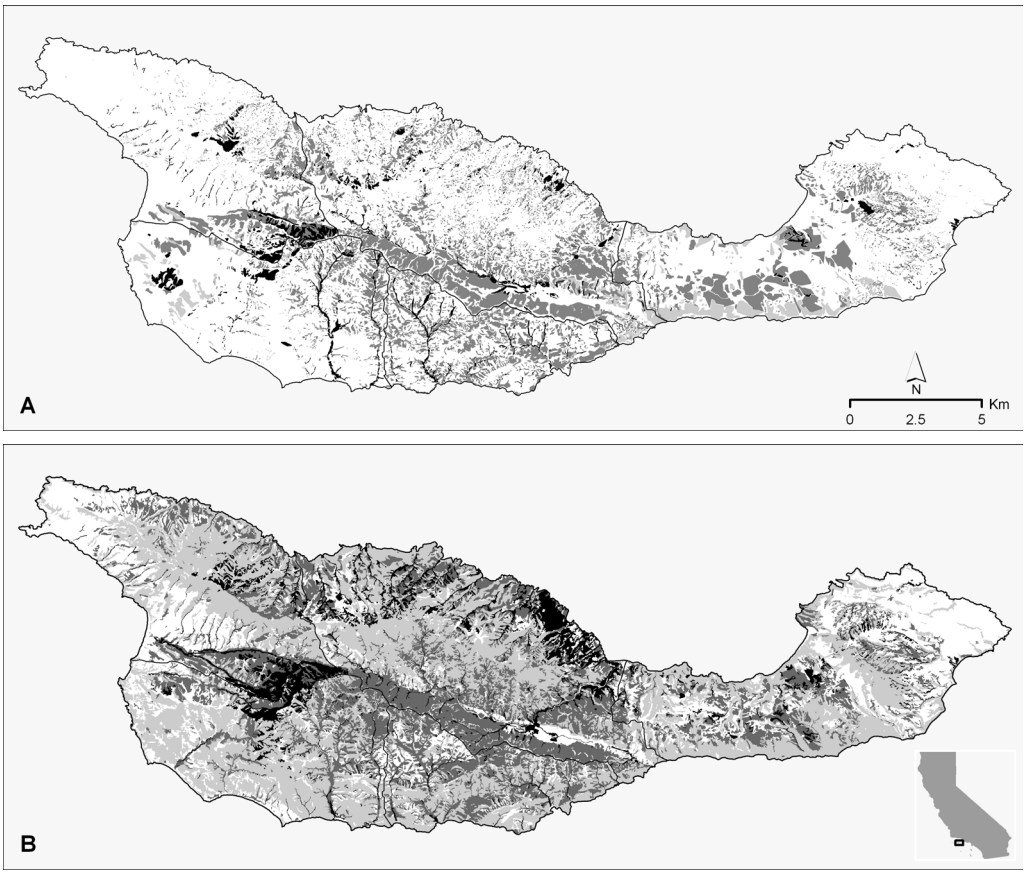

Figure 1. Vegetation change on Santa Cruz Island, 1985–2005. Maps depict generalized vegetation categories: bare ground and herbaceous vegetation, white; scrub and low stature vegetation, light gray; chaparral and medium canopy communities, dark gray; forest and woodland, black. (A) Vegetation prior to/during the eradication of feral sheep (adapted from Jones et al. 1993 and Howarth et al. 2005). (B) Vegetation of 2005. Island location in the state of California shown in inset.

sometime in the mid- to late 1800s. By 1887 it was thoroughly established on the hillsides around Prisoners' Harbor (Junak et al. 1995). Sheep and cattle grazed fennel and spread seeds in their feces and on their hooves. Pig wallows and rooting were numerous in fennel areas (B. Cohen, C. Cory, and J. Menke, personal observation 2006), and pigs were also likely vectors for seeds. It is interesting to note that while sheep and cattle were present, fennel was kept low enough in stature to not be noticed or categorized in previous vegetation maps (Minnich 1980; Jones et al. 1993). With removal of cattle in the mid-1990s, fennel became more conspicuous in the landscape. The current database designates a separate category for fennel-dominated areas (AIS 2007). These fennel polygons were also assigned cover categories. Future vegetation mapping can thus track the extent and cover of fennel. Decreasing fennel cover can indicate recolonization by other plants.

Conservation organizations and agencies spend a great deal of public and private money protecting and restoring elements of biodiversity. On SCI this has included removal of feral non-native animals and invasive weed species as well as supporting projects to increase the numbers of native foxes, bald eagles, and rare plants. Tracking and monitoring results and consequences of these actions also require a significant investment of time and money. For land managers of SCI, this type of vegetation map and database represents a cost-effective way to monitor long-term changes across a large landscape. Traditional ground-based vegetation monitoring methods using plots, transects, relevés, etc., can be extremely costly in terms of staff time. While such ground-based data may be very detailed, they are limited in spatial scale, and often limited in scope due to rugged or inaccessible terrain. Unlike vegetation mapping based on plot data that must then be extrapolated to areas not sampled, the methodology presented here essentially samples the entire landscape and provides relatively fine-scale information for any given point on the island. We believe that by employing both fine-scale field methods and larger scale photo-based methods, we have developed a highly sensitive and cost-effective means of monitoring changes to vegetation across a landscape within a broad range of scales.

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Appendix . Distribution of vegetation on Santa Cruz Island at all levels of classification.

Class	Formation	Mapping unit or alliance	Sub alliance – Potential associations	Hectares	% of island	% of class	% of formation
1000 – Forest							
	1100 – Temperate Broadleaf Sclerophyll Evergreen Forests			0.1	0.0%	0.0%	0.0%
		1110 – Ironwood Alliance		178.9	0.7%	19.1%	70.2%
		1120 – Eucalyptus Stands Mapping Unit		31.7	0.1%	3.4%	12.4%
		1130 – Island Cherry - (Island Scrub Oak – Toyon)		44.3	0.2%	4.7%	17.4%
	1200 – Temperate Needleleaf Evergreen Forests						
		1201 – Introduced Pines or Cypress Mapping Unit		0.9	0.0%	0.1%	0.1%
		1210 – Bishop Pine Alliance		106.6	0.4%	11.4%	16.1%
			1211 – Bishop Pine –(Island Oak) / (Summer Holly – Toyon)	254.2	1.0%	27.1%	38.3%
			1212 – Bishop Pine / California Huckleberry – (Summer Holly-Toyon)	5.5	0.0%	0.6%	0.8%
			1213 – Bishop Pine / Island Scrub Oak – Island Manzanita	223.4	0.9%	23.8%	33.6%
			1214 – Bishop Pine / Island Scrub Oak – (McMinn's Manzanita – Woolly Leaf Manzanita)	21.1	0.1%	2.3%	3.2%
			1215 – Bishop Pine – Coast Live Oak / (Island Scrub Oak–Island Manzanita)	52.4	0.2%	5.6%	7.9%
	1300 – Temporarily Flooded Cold Season Deciduous Forests			0.5	0.0%	0.1%	2.5%
		1310 – Big Leaf Maple Alliance		1.8	0.0%	0.2%	9.3%
		1320 – Fremont Cottonwood – Black Cottonwood Superalliance		16.9	0.1%	1.8%	88.3%
	Forest Total			**938.1**	**3.8%**		
2000 – Woodlands							
	2100 – Xeric Sclerophyll Evergreen Woodlands						
		2110 – Coast Live Oak Alliance		660.5	2.7%	99.1%	99.1%
		2120 – Canyon Live Oak Alliance		5.7	0.0%	0.9%	0.9%
	Woodlands Total			**666.2**	**2.7%**		
3000 – Shrublands				4.4	0.0%	0.0%	0.0%
	3100 – Temperate Broadleaf Sclerophyll Evergreen Shrublands (Chaparral)			84.5	0.3%	0.5%	1.7%
		3101 – McMinn's Manzanita - (Woolly Leaf Manzanita)		13.2	0.1%	0.1%	0.3%

Appendix (continued). Distribution of vegetation on Santa Cruz Island at all levels of classification.

Class	Formation	Mapping unit or alliance	Sub alliance – Potential associations	Hectares	% of island	% of class	% of formation
		3110 – Chamise Alliance		19.3	0.1%	0.1%	0.4%
		3120 – Island Scrub Oak Alliance		720.3	2.9%	4.1%	14.1%
			3121 – Island Scrub Oak – Island Manzanita (Chamise - Bigpod Ceanothus)	1201.0	4.8%	6.9%	23.5%
			3122 – Island Scrub Oak – Summer Holly	45.4	0.2%	0.3%	0.9%
			3123 – Island Scrub Oak – Island Ceanothus	1687.2	6.8%	9.7%	33.0%
			3124 – Island Scrub Oak – (Island Manzanita – Chamise–Bigpod Ceanothus) Maritime	136.4	0.5%	0.8%	2.7%
			3125 – Island Scrub Oak – McMinn's Manzanita – (Woolly Leaf Manzanita – Chamise)	204.5	0.8%	1.2%	4.0%
			3126 – Island Scrub Oak – Coastal Sage Scrub Transition	562.0	2.3%	3.2%	11.0%
		3130 – Island Manzanita Alliance		213.9	0.9%	1.2%	4.2%
		3140 – Birch-leaf Mountain Mahogany Alliance		11.8	0.0%	0.1%	0.2%
		3150 – Lemonadeberry Alliance		209.4	0.8%	1.2%	4.1%
	3200 – Temperate Microphyllous Evergreen Shrublands						
		3240 – Coyote Brush Alliance		986.6	4.0%	5.7%	87.5%
		3250 – Mulefat Alliance		140.8	0.6%	0.8%	12.5%
	3300 – Temperate Xeric Mixed Drought-Deciduous Shrublands			10.8	0.0%	0.1%	0.1%
		3301 – Coastal Bluff Scrub Habitat		650.3	2.6%	3.7%	6.0%
		3302 – Australian Saltbush Mapping Unit		112.6	0.5%	0.6%	1.0%
		3303 – Inland Bluff Scrub Habitat		2716.0	10.9%	15.6%	24.9%
		3310 – California Sagebrush Alliance		650.3	2.6%	3.7%	6.0%
			3311 – California Sagebrush Pure Stands	7.9	0.0%	0.0%	0.1%
			3312 – California Sagebrush – Santa Cruz Island Buckwheat	980.7	3.9%	5.6%	9.0%
			3313 – California Sagebrush – Lemonadeberry	804.1	3.2%	4.6%	7.4%
			3314 – California Sagebrush - Coastal Bluff Scrub Transition	276.6	1.1%	1.6%	2.5%

Appendix (continued). Distribution of vegetation on Santa Cruz Island at all levels of classification.

Class	Formation	Mapping unit or alliance	Sub alliance – Potential associations	Hectares	% of island	% of class	% of formation
			3315 – California Sagebrush – Island Bush Monkeyflower	349.9	1.4%	2.0%	3.2%
			3316 – California Sagebrush – Coyote Brush	357.4	1.4%	2.1%	3.3%
		3320 – Santa Cruz Island Buckwheat Alliance		2634.2	10.6%	15.1%	24.2%
		3330 – Saint Catherine's Lace Alliance		56.5	0.2%	0.3%	0.5%
		3340 – Island Bush Monkeyflower - Island Bristleweed – Paintbrush Mapping Unit		1291.0	5.2%	7.4%	11.8%
	3400 – Temporarily Flooded Cold Season Deciduous Shrublands			1.4	0.0%	0.0%	0.6%
		3401 – Mixed Arroyo Willow – Mule Fat Mapping Unit		178.4	0.7%	1.0%	76.7%
		3410 – Arroyo Willow Alliance		53.0	0.2%	0.3%	22.8%
	Shrublands Total			**17,404.2**	**69.8%**		
4000 – Herbaceous				0.3	0.0%	0.0%	0.1%
	4100 – Saturated Temperate Perennial Graminoids						
		4101 – Bulrush – Cattail Mapping Unit		0.1	0.0%	0.0%	100.0%
	4200 – Seasonally or Temporarily Flooded Graminoids						
		4201 – Seasonally or Temporarily Flooded Springs, Seeps, Vernal Ponds Mapping		0.8	0.0%	0.0%	100.0%
	4300 – Tall Temperate Annual Graminoids			24.8	0.1%	0.5%	0.5%
		4301 – Fennel Mapping Unit		244.9	1.0%	4.6%	4.8%
		4310 – California Annual Grasslands Alliance		4817.9	19.3%	91.2%	94.5%
		4320 – Giant Wildrye - Creeping Wildrye Superalliance		8.6	0.0%	0.2%	0.2%
	4400 – Tall Temperate Perennial Graminoids						
		4401 – Coastal Salt Pan Mapping Unit		1.7	0.0%	0.0%	3.0%
		4402 – Needlegrass					0.0%
		4410 – Silver Beachbur - Beach Sand-Verbena Alliance		20.5	0.1%	0.4%	37.4%
		4420 – Harding Grass		32.6	0.1%	0.6%	59.6%
	4600 – Tidally Flooded Grasslands			1.3	0.0%	0.0%	2.1%
		4610 – Saltgrass Alliance		59.3	0.2%	1.1%	97.9%
	4700 – Tall Temperate Forblands			7.6	0.0%	0.1%	7.4%
		4701 – Sea Blite – San Miguel Island Locoweed		28.3	0.1%	0.5%	27.7%
		4702 – Tejon Milk Aster - (Coastal Goldenbush)		62.3	0.3%	1.2%	60.8%

Appendix (continued). Distribution of vegetation on Santa Cruz Island at all levels of classification.

Class	Formation	Mapping unit or alliance	Sub alliance – Potential associations	Hectares	% of island	% of class	% of formation
		4710 – Bracken Fern Alliance		4.2	0.0%	0.1%	4.1%
	Herbaceous Total			**5325.0**	**21.3%**		
9000 – Land Use – Sparsely or Unvegetated							
	9100 – Built-up			30.4	0.1%	5.0%	100.0%
	9400 – Sparsely Vegetated or Unvegetated Areas			6.8	0.0%	1.1%	1.2%
		9410 – Landslides		12.9	0.1%	2.1%	2.3%
		9420 – Cliffs – Rock Outcrops – Steep eroded slopes		510.1	2.0%	83.7%	89.6%
		9430 – Stream Beds and Flats		39.8	0.2%	6.5%	7.0%
	9600 – Planted trees & shrubs			9.5	0.0%	1.6%	100.0%
	Land Use – Sparsely or Unvegetated Total			**609.5**	**2.4%**		

Pages 245–252 in Damiani, C.C. and D.K. Garcelon (eds.). 2009. Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.

SANTA CRUZ ISLAND INVASIVE PLANT SPECIES MAP

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Abstract—Effectively managing non-native invasive plants at a landscape scale requires an understanding of species distribution and abundance. Oftentimes land managers lack population data on which to base long-term management decisions, resulting in shifting priorities and the squandering of scarce resources. In 2007, The Nature Conservancy (TNC) contracted Prohunt Incorporated to conduct an island-wide survey of 55 invasive plant species on Santa Cruz Island, a 243 km^2 island jointly owned and managed by TNC and the Channel Islands National Park. This inventory differed from other invasive plant surveys in that the entire island was searched in person, and populations were mapped with a global positioning system. The survey was completed in 41 days. Approximately 95% of the survey was conducted from a helicopter operating between 1.5 and 9 m above ground; the remaining 5% was surveyed by two or more mappers walking parallel to each other along drainages and heavily infested areas to maximize species detection. Aerial surveys used in concert with ground surveys are a fast and effective method for early detection which can provide key data to develop comprehensive management plans, and it has the potential to be utilized for rapid response in remote sites such as offshore islands.

INTRODUCTION

Invasive species are considered the second greatest threat to biodiversity worldwide, and are the leading cause of species extinctions in island ecosystems (Wilson 1999). Invasive plants are a significant factor affecting the preservation of native biodiversity—one of the major challenges of this century (D'Antonio and Meyerson 2002). Land managers entrusted with protecting natural resources must often manage weeds through a form of triage, where they hastily identify which species will be targeted for control and which ones will be left to possibly spread. These decisions are often based on anecdotal and unverified data (P. Holloran 2006, U.C. Santa Cruz Environmental Studies Department, personal communication). Diverting limited resources to survey and inventory weed populations might appear to be a waste of time and money when the impacts caused by weeds are readily apparent. Yet land managers often function as physicians who are entrusted with healing their patient (the land), and a good doctor should give his or her patient a proper examination before prescribing a remedy to cure an illness (Knapp and Knapp 2005). Likewise, a proper inventory of local weed populations can provide a sound scientific foundation for future management actions.

Weed infestations are never static, and there are often too many to keep track of with the human brain. If key species and population information are not recorded in a database, that organizational knowledge can easily be lost when the land manager relocates or dies. The epitaph of a land manager's tombstone could read, "Here lies all the institutional weed knowledge of the preserve." (Schoenig et al. 2002). By creating a computer database of weed populations, key information on abundance, distribution, and rates of spread will be readily available to all future weed managers who will be able to use it to analyze changes in populations, develop monitoring schedules, evaluate control efficacy, and record the appearance of new populations in the long term.

Invasive species are the greatest threat to Channel Island ecosystems as a whole (Donlan et al. 2003). During the period of intensive ranching and crop production from the 1840s to 1980s, many invasive plant species became established on Santa Cruz Island (SCI), the largest (24,864 ha) of the

eight California Channel Islands. The weeds were largely held in check by cattle, sheep, and pigs. However, they appear to have been released from browsing and grazing pressure following the recent removal of these introduced ungulates by the Channel Islands National Park (CINP), who owns 24% of the island, and The Nature Conservancy (TNC), a non-profit conservation organization that owns and manages 76% of the island.

TNC has conducted select treatments and control experiments for a suite of weed species since the early 1990s (R. Klinger, U.S. Geological Survey Biological Science Division, personal communication), and is currently in the process of developing an invasive plant management plan and program to comprehensively address the next greatest conservation challenge—large-scale weed eradication and control. One of the main objectives of TNC's developing weed program is to target priority weeds that are now in limited abundance before they become widespread and unmanageable species. TNC contracted Prohunt Incorporated (Ventura, California) to survey the entire island for 55 weed species, to develop a detailed baseline of the current state of weed abundance and distribution on the island. This map will provide the foundation for the development of TNC's Santa Cruz Island Weed Management Strategy, enabling managers to prioritize each species for eradication, reduction, or control by systematically evaluating each species based on their known impacts, invasiveness, distribution, and abundance. In this paper, we describe the island-wide survey of Santa Cruz Island, and the construction of the weed map.

METHODS

The reference *A Flora of Santa Cruz Island* by Junak et al. (1995) identifies over 177 naturalized non-native plants on Santa Cruz Island, and served as the baseline dataset of known taxa on the island. The list also contains a few species known to exist on adjacent Channel Islands but not yet recorded from SCI (e.g., *Delairea odorata*). Not all 177 non-native plant species are considered to be invasive or a threat to the island. The objective of TNC's invasive plant management program is to address species that pose the greatest risk to the island, but are also relatively manageable. The list of 177 non-native species were compared with the California Invasive Plant Council's (Cal-IPC) "Invasive Plant Inventory" of weeds in California (Cal-IPC 2006) in order to derive a preliminary list of 111 invasive weed species found on the island. The winter of 2006–2007 delivered very little rain to Santa Cruz Island, and some herbaceous plants, both native and non-native, were not conspicuous in the landscape in the spring of 2007. These species were thus removed from the list of 111 species considered for the survey.

The Delphi method (Matlack 2002) was utilized to narrow down which of the remaining weed species posed the greatest risk to the island, and are considered manageable (for instance, species such as Mediterranean annual grasses are highly invasive, but were considered to be unmanageable at the landscape level due to their widespread distribution and abundance). The Delphi method involves submitting a list of suspected weed species to qualified individuals such as botanists, plant ecologists, weed scientists, and land managers for review based on their professional experience. Of the 14 individuals invited to submit suggestions, 7 submitted species candidates, while others acknowledged the selections of others. The list was then narrowed by managers from TNC and the CINP, who identified 55 weed species that would be appropriate for an island-wide survey. The 55 weed species selected are known to negatively affect wildlands, and could be detected from the air and on the ground by surveyors during the time period of the survey. Fifty-five species were considered to be the maximum number of targets that surveyors could easily scan for and keep track of while conducting the survey.

Survey methods previously utilized to map 76 weed species on Catalina Island in 2003 (Knapp 2004) were adapted for the island-wide weed survey on Santa Cruz Island. A discrete weed population was defined by a distance of 30.5 m (100 ft) from one population edge to another or between two single plants. This distance between populations is approximately the greatest distance at which a ground surveyor can detect low growing small individual weeds. The minimum mapping unit was an individual plant. Ground and aerial surveyors visually estimated population size and density in square feet, phenology, plant height, and habitat type invaded, and each population was recorded

with a sub-meter accuracy Trimble GeoExplorer® Series global positioning system (GPS). All populations were captured as point or line features with a GPS at a speed of 10 to 30 seconds per infestation.

A significant difference from the previous mapping methodology was the use of a two-person Schweizer 300 helicopter owned and piloted by Prohunt Incorporated. Initially, the three-month survey was to be conducted 80% from the ground by five mappers, with the remaining inaccessible areas (20%) such as coastal bluffs to be surveyed from the air with a helicopter. During the first hour of flight over island chaparral and coastal scrub communities, it became clear that the perspective from the helicopter provided a superior vantage point from which to survey vegetation. A greater area could be covered in less time. Thereafter, it was decided to survey as much of the island from the air as possible, and the ground mappers would be redirected to survey roadsides, developed areas, and sites with a large number of weed species and infested areas. The survey was conducted continuously from April 2 to May 13, 2007, only 41 days, with 95% of the island surveyed from the air and 5% from the ground.

Approximately 4281 linear km (2660 miles) (Fig. 1) were surveyed across the entire island. The aerial survey, covering 3349 linear km (2081 miles), was flown at altitudes between 1.5 and 9.1 m (5 to 30 ft) above the ground. The height of the helicopter was determined by topography, weather, and vegetation. A trained mapper recorded weed locations and indicated to the pilot when a better vantage point was required to assure weed identification. The helicopter was flown between 13 to 17.4 knots (15 to 20 mph), but would hover when confirming species identification, and mapping. Ground surveys covering 932 linear km were conducted by two or more trained ground mappers walking abreast of one another to ensure maximum species detection.

In addition to recording species infestations in the Trimble GeoExplorer® GPS units, all ground mappers carried a Garmin® Foretrex™ 201 GPS, and the helicopter was equipped with a Garmin®

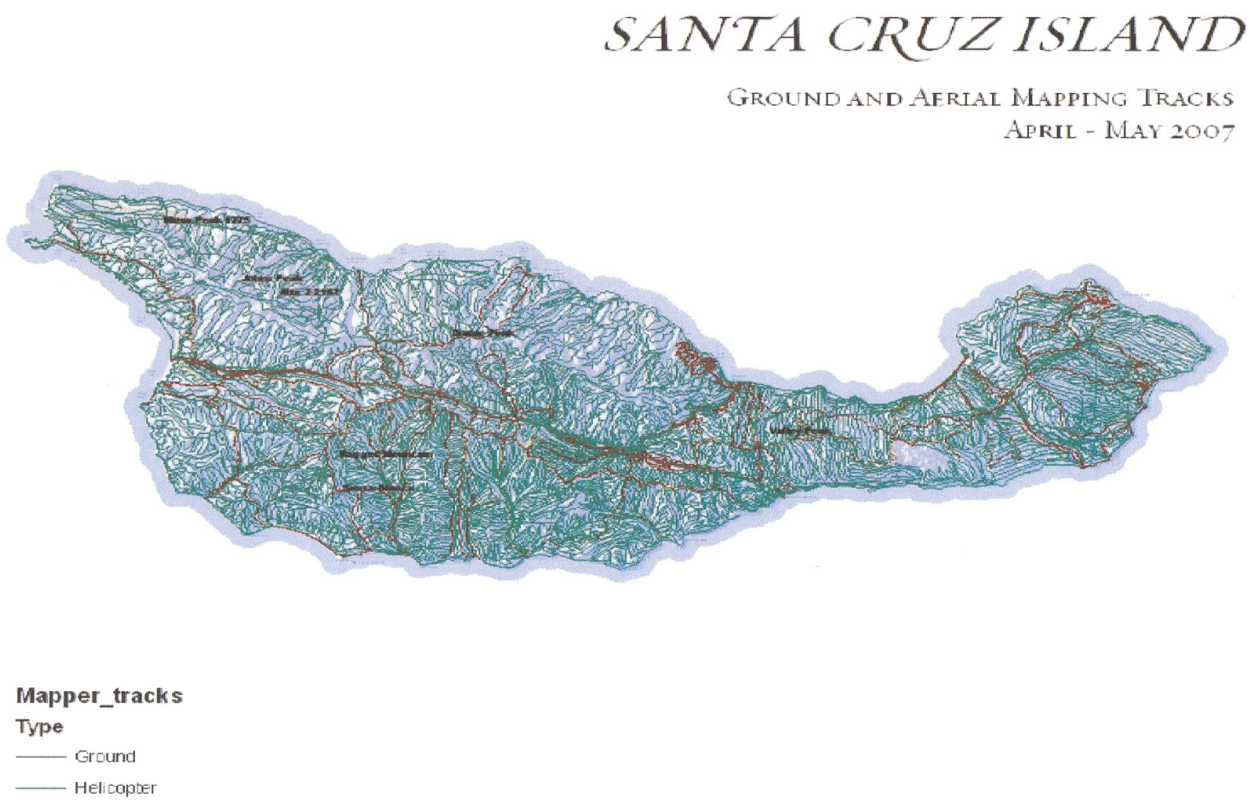

Figure 1. A map illustrating the aerial (green lines) and ground (brown lines) survey tracks.

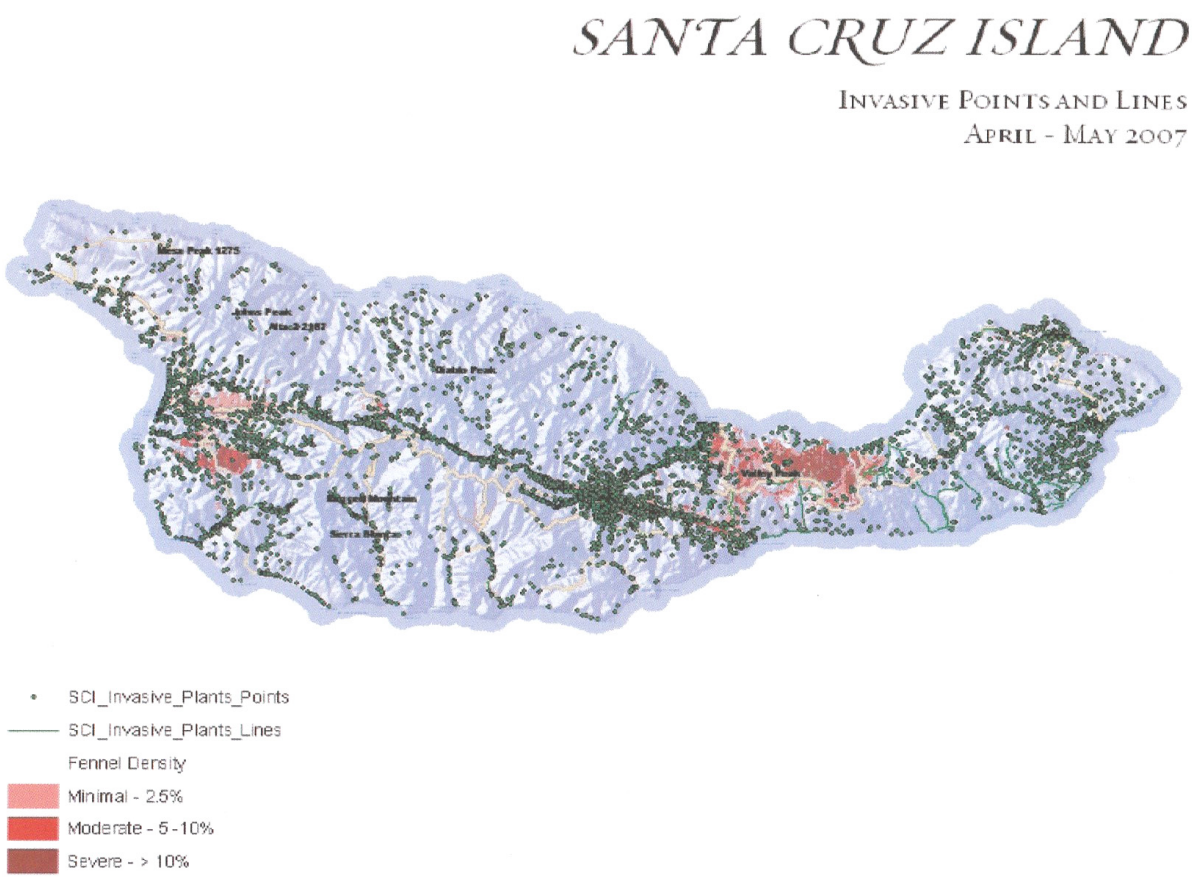

Figure 2. A map illustrating the locations of 52 invasive plant species.

GPSMAP® 196 to record survey routes as line features. Survey tracks were used to identify gaps in area not surveyed, which were then flown the following day.

All points and line features were entered each evening in a Geographic Information System geodatabase (ESRI, ArcMap 9.2, Redlands, CA) and were reviewed for missing or duplicate data. Any anomalies were then addressed the following survey day. The final geodatabase was then submitted to TNC, who then co-developed with NPS, a database to record future weed infestations and weed treatments.

RESULTS

A total of 5942 populations were recorded among 52 weed species (Fig. 2). Table 1 illustrates each species surveyed, along with the associated number of populations and net area infested (area infested multiplied by the density of weeds). Of the 55 species selected for survey, three species (*Araujia sericifera, Delairea odorata,* and *Ricinus communis*) were not detected. The only previously known population of *Araujia sericifera* (bladder flower) was removed by the Channel Islands National Park prior to the survey (S. Chaney 2007, Channel Islands National Park, personal communication). The latter two species had not been seen on the island for several years, but were surveyed for nonetheless due to their invasiveness on the mainland. One new species was recorded for the island, *Cynara cardunculus* (artichoke thistle), consisting of only one population.

DISCUSSION

Invasive plant management decisions are often based solely on the threat(s) the species pose, because obtaining detailed distribution and

Table 1 . Surveyed weed species population data.

Weed species	Number of populations	Net area (m2)	Median population size (m2)
Acacia dealbata	1	136	N/A
Acacia melanoxylon	56	2,284	2
Albizia lophantha	15	529	21
Araujia sericifera	0	0	0
Arundo donax	8	80	20
Cakile maritima	142	4,200	52
Cardaria draba	133	15,886	209
Carduus pycnocephalus	1	418	N/A
Carpobrotus chilensis	140	3,486	37
Carpobrotus edulis	1	0.09	N/A
Centaurea solstitialis	313	91,408	47
Centranthus ruber	7	143	112
Cirsium vulgare	2	2	N/A
Conium maculatum	19	172	11
Cortaderia selloana	98	746	0.4
Cupressus macrocarpa	26	10,703	2
Cynara cardunculus	1	3,832	N/A
Delairea odorata	0	0	0
Ehrharta erecta	2	2	N/A
Erechtites glomerata	146	95	0.09
Eriogonum giganteum	8	592	3
Eucalyptus camaldulensis	43	95,096	0.09
Eucalyptus globulus	72	58,654	60
Festuca arundinacea	2	2	N/A
Ficus carica	23	219	0.09
Foeniculum vulgare	1,837	325,983	23
Genista monspessulana	28	54	0.09
Hedera canariensis	16	1760	7
Juglans regia	29	0.09	0.09
Lavatera assurgentiflora	9	388	3
Mesembryanthemum	46	246	9
Nicotiana glauca	177	80,024	232
Olea europaea	105	107,796	0.09
Opuntia ficus-indica	2	13	N/A
Pelargonium X hortorum	20	66	2
Pennisetum clandestinum	48	30,862	84
Phalaris aquatica	161	272,385	37
Phoenix canariensis	2	0.002	N/A
Pinus pinea	48	4607	2
Piptatherum miliaceum	406	16,246	37
Ricinus communis	0	0	0
Robinia pseudoacacia	15	1,359	2
Rubus armeniacus	11	142	9

Table 1 (continued). Surveyed weed species population data.

Weed species	Number of populations	Net area (m2)	Median population size (m2)
Salsola tragus	62	23,468	149
Schinus molle	178	3,569	2
Silybum marianum	679	22,027	37
Solanum elaeagnifolium	1	1	N/A
Spartium junceum	3	35	0.09
Tamarix ramosissima	50	1,801	0.09
Tetragonia tetragonioides	11	6	1
Verbascum thapsus	604	81,978	9
Vinca major	31	9,937	19
Washingtonia robusta	7	0.09	0.09

abundance data for a suite of species has been cost-prohibitive until now. Knowledge of the threats posed by a species coupled with its population data can be powerful decision making tools to guide long-term management, and are key elements of TNC's Santa Cruz Island Weed Management Strategy. Highly invasive abundant widespread species such as *Foeniculum vulgare* (fennel) or *Centaurea solstitialis* (yellow star thistle) may not be candidates for eradication in the near future, but they could be systematically targeted along dispersal corridors to reduce their spread, and/or in priority watersheds where high-value resources are at risk, which is where TNC is currently managing them. Highly invasive species that have few small populations with undeveloped soil seed banks such as *Carduus pycnocephalus* (Italian thistle), *Cortaderia selloana* (Pampas grass), or *Eriogonum giganteum* var. *giganteum* (Saint Catherine's lace) are ideal candidates for eradication, and are currently being managed for these reasons. Baseline distribution and abundance data on invasive plants could be compared with data collected from future surveys to determine the rate of spread of existing species, and the rate of colonization of new species. Even more powerful analyses can be conducted to evaluate which vegetation communities are most susceptible to invasion, or which sites have the greatest number of new colonizers over time, and thus priority sites to monitor.

A study conducted by Rejmanek and Pitcairn (2002) analyzed weed eradication efforts conducted by the California Department of Food and Agriculture over a 30-year period. Results showed that weed eradication success decreased exponentially and the effort (time, money, etc.) increased exponentially as the size of the weed infestation increased. They also found that infestations less than 0.08 ha had nearly 100% eradication success, and that infestations 1 ha and greater had nearly no eradication success. The median population size of the 52 weed species recorded (excluding three species not detected) in spring 2007 was 0.0008 acres; however, this size will not remain static as these highly invasive species continue to expand.

Species that have recently colonized SCI or are becoming established are a high priority for TNC, because these species are relatively easy and cost-effective to eradicate (Zavaleta et al. 2001), and their impacts are minor compared to widespread species (Zavaleta 2000). Species that have small populations are much easier to eradicate than larger ones, due to the limited soil seed bank present.

Advanced techniques and methods to remove non-native feral ungulates have recently been developed and successfully implemented (Morrison 2007; Donlan et al. 2003), and similar techniques need to be developed for successful plant eradications (Donlan et al. 2003). Aerial transport of personnel and equipment by helicopter has played an important role in managing Santa Cruz Island and implementing conservation projects. Projects like the removal of feral pigs in 2005–2006, and the Island-wide Weed Mapping Survey in April 2007 have shown how useful a helicopter can be in remote terrain that is difficult or dangerous to access on the ground, in areas where vegetation impedes ground transportation, or where weed seed might readily be dispersed by ground access.

A helicopter, especially one as small and maneuverable as the one utilized in this survey, and

a highly qualified bush pilot are probably the most effective tools to use for early detection of and rapid response to new weed invasions. A helicopter can provide a perfect vantage point from which to locate an infestation and the means by which to respond quickly to eliminate it. Hiking to remote weed infestations can expend a great deal of time and effort, dispersing weed seed along the access route, and damage recovering or intact vegetation, resulting in erosion. Aerial transport can eliminate these impacts by avoiding contact with weed propagules and taking the weed worker directly to the site. Using a helicopter is also a cost-effective method of surveying the island. The survey was completed in 41 days. When compared to an estimate to conduct the same project with only ground surveyors, the aerial survey is half the cost of a ground-based survey and can be completed approximately eight times more quickly.

The ability of land managers to detect infestations and stay ahead of seed production is a difficult obstacle to overcome when managing invasive plants, but using a helicopter to access infestations allows land managers to exceed the pace of weed seed production and to continually survey the landscape. The most cost-effective method to address weeds is to prevent them before they colonize or become established (Zavaleta 2000). Preventing species introduction or establishment will also eliminate impacts to the ecosystem. Implementing early detection and rapid response programs enable land managers to eliminate future problems by tackling them while they are at manageable levels.

CONCLUSIONS

Following the elimination of landscape-level disturbances caused by introduced ungulates, Santa Cruz Island land managers are entering a new era of island-wide vegetation management and protection. Non-native invasive plant species pose a significant threat to the recovery and integrity of the island ecosystem. The Channel Islands National Park has worked diligently over the last two decades to tackle these threats, and now The Nature Conservancy is dedicating significant resources to weed management.

The results of the island-wide weed survey conducted in the spring of 2007, has provided TNC and CINP with information needed to develop a comprehensive weed management program and strategy. The 2007 SCI Weed Map identified which species can likely be eradicated (based on limited ranges and population sizes) and which ones require a more strategic watershed-based approach. An extensive database of weed distributions and abundance and a comprehensive weed management strategy are in development as a result of this weed survey. Coordinated implementation programs will enable the SCI land managers to effectively tackle the invasive weed crisis island-wide.

Prior to this survey, land managers of large preserves lacked an accurate and cost-effective method to develop a weed distribution and abundance baseline, which includes individual plants and large infestations. The aerial survey methods developed by TNC staff, their project advisor, and contractor Prohunt, Inc. now provide an effective method for land managers to systematically conduct early detection and rapid response programs, especially on other offshore islands.

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FOOD HABITS OF NESTING GOLDEN EAGLES (*AQUILA CHRYSAETOS*) ON SANTA CRUZ AND SANTA ROSA ISLANDS, CALIFORNIA

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Abstract—Between 2000 and 2007, we studied food habits of golden eagles (*Aquila chrysaetos*) nesting on Santa Cruz and Santa Rosa islands by analyzing prey remains recovered from 11 nests—7 on Santa Cruz Island and 4 on Santa Rosa Island. We collected 464 prey items representing 28–30 species. Based on biomass, the most important prey for golden eagles before feral pigs (*Sus scrofa*) were eradicated from the islands were feral piglets (31.4%), mule deer (*Odocoileus hemionus*) fawns and elk (*Cervus elaphus*) calves (18.0%), common raven (*Corvus corax*; 17.4%), cormorants (*Phalacrocorax* sp.; 10.3%), and gulls (*Larus* sp. 6.7%). There were island-specific differences both in species and biomass of prey. On Santa Cruz Island, the eagles' diet consisted of feral pigs (63.2%), gulls (13.3%), and common ravens (8.9%); while on Santa Rosa Island the eagles' diet consisted of mule deer fawns (34.6%), common raven (25.8%), cormorants (14.2%), and waterfowl (8.6%). Prior to removal of feral pigs, island foxes (*Urocyon littoralis*) and feral piglets comprised 5.9% and 63.2% of the biomass found in the eagle nests on Santa Cruz Island; however after removal of feral pigs, we found a greater proportion of island foxes (45.7–57.7%), common ravens (24.7–26.7%), and gulls (18.0–19.5%) in the nest remains. The depauperate nature of the vertebrate prey on the islands has resulted in golden eagles foraging on a number of prey species not typically eaten by eagles elsewhere in North America such as island fox, western spotted skunk (*Spilogale gracilis*), feral piglets, mule deer fawns, common raven, barn owl (*Tyto alba*), gulls, and cormorants.

INTRODUCTION

Until the early 1980s, golden eagles (*Aquila chrysaetos*) were an occasional visitor to the larger islands off the coast of southern California, with the majority of records from Santa Cruz Island (SCI) (Collins and Jones, unpublished manuscript). By the late 1980s and early 1990s, sightings of golden eagles on SCI had increased, suggesting that they were becoming established as a year-round resident. They were first recorded to breed on SCI with the discovery of a nest at Coche Point in 1999 (Roemer et al. 2001; Latta et al. 2005). Since then, a total of 29 large, eagle-sized nest structures have been discovered in at least five eagle territories on SCI and four nests have been found in two eagle territories on Santa Rosa Island (SRI) (Latta et al. 2005). Multiple nests within an eagle's territory and nests with up to four distinct nest layers suggest that golden eagles have been nesting on SRI since at least the mid-1990s and on SCI since at least the early 1990s (Latta et al. 2005).

Golden eagles have been implicated in the catastrophic decline of island fox (*Urocyon littoralis*) populations on three of the northern Channel Islands between 1994 and 1999 (Roemer et al. 2001, 2002; Coonan et al. 2002; Coonan, Schwemm, et al. 2005; Roemer and Donlan 2004). To stem this population decline, the National Park Service (NPS) and The Nature Conservancy (TNC) implemented a series of emergency recovery actions including: (1) a trapping and relocation program for golden eagles; (2) establishment of on-island captive breeding programs for island foxes; (3) a reintroduction program for bald eagles (*Haliaeetus leucocephalus*) to the northern Channel Islands; and (4) an eradication program for feral pigs (*Sus scrofa*) on SCI. In 2004 the U.S. Fish and Wildlife Service (USFWS) listed four island fox subspecies as endangered, including the three found on the northern Channel Islands (USFWS 2004). As a result of these recovery actions, a total of 44 golden eagles were live-captured and translocated from the islands to the mainland (Coonan,

McCurdy, et al. 2005; Latta et al. 2005; IWS 2006); a total of 61 bald eagles were released onto SCI (Dooley et al. 2005; Coonan and Dennis 2007); island fox populations on the northern Channel Islands were protected from extinction; and by mid-2006 feral pigs were eradicated from SCI (MacDonald and Walker 2008). Because of the success of each of these conservation measures, TNC began releasing island foxes back onto SCI in 2002 and 2003, and the NPS began releases of island foxes on SRI in fall 2003 and on San Miguel Island (SMI) in fall 2004 (Coonan, McCurdy, et al. 2005). Despite intensive golden eagle translocation efforts, a few eagles remain on Santa Cruz and Santa Rosa islands where they continue to prey on island foxes (IWS 2006).

There have been numerous food habit studies of golden eagles from throughout their range in North America (see summaries in Olendorff 1976 and Kochert et al. 2002) and from elsewhere in Europe and Asia (see Table 9 in Watson 1997). While food habits of golden eagles are reasonably well documented for several western states (McGahan 1968; Arnell 1971; Boag 1977; Collopy 1983; Marr and Knight 1983; Eakle and Grubb 1986; MacLaren et al. 1988), there are only a few studies that provide any data on the food habits of golden eagles in California (Dixon 1937; Carnie 1954; Bloom and Hawks 1982; Hunt et al. 1995) and only three studies that provide data on the food habits of island-inhabiting populations of golden eagles (Grubac 1987; Hogstrom and Wiss 1992; Watson 1997). Until recently there were only anecdotal observations of the eagles' diet on the Channel Islands. Collins and Latta (2006) provided the first quantitative assessment of the diet of golden eagles on Santa Cruz and Santa Rosa islands based on prey remains recovered from eight nests. The present study combines data from three new nests not previously sampled, with the original sample of eight nests analyzed by Collins and Latta (2006).

Golden eagles are opportunistic specialists that prey on a wide variety of types and sizes of prey (Olendorff 1976; Kochert et al. 2002). In western North America they tend to feed on whatever is most readily available in a particular region, generally rabbit and squirrel-sized prey that they can overpower easily. They also feed on carrion, primarily during the winter, and occasionally kill larger prey including a variety of native ungulates and domestic animals such as sheep (*Ovis aries*), goats (*Capra hircus*), calves (*Bos tarus*), and pigs (Olendorff 1976; Kochert et al. 2002). Golden eagles generally take young ungulates but have also been known to kill adults (Deblinger and Alldredge 1996). Based on averaging the results (minimum number of individuals, MNI) from 18 food habit studies, the diet of nesting golden eagles in western North America is composed of 76.7% (MNI) terrestrial mammals, 20.5% birds, 1.6% reptiles, and 0.5% fish (see Appendix 1 in Collins and Latta 2006). During the nesting season they feed primarily on leporids (hares and rabbits) and sciurids (ground squirrels, prairie dogs, and marmots) comprising between 49 and 94% of prey items recovered in food habit studies throughout western North America (Kochert et al. 2002). They also feed less intensively on a variety of birds, with gallinaceous species (pheasants, grouse, and partridge) being the most common, and occasionally on reptiles (snakes) and fish (Olendorff 1976; Kochert et al. 2002).

Most recent studies of golden eagle food habits have relied on the identification of prey remains recovered from regurgitated food pellets and from prey remains collected at nests and perches (see references cited in Olendorff 1976; Watson 1997; Kochert et al. 2002). Recently, Caut et al. (2006) used stable isotopes coupled with bioenergetics to estimate the interspecific interactions of golden eagles, island foxes, spotted skunks, and feral pigs on SCI. Without quantified food habit data, it is impossible to fully understand the extent of interspecific interactions of golden eagles with the vertebrate fauna on the Channel Islands. Thus, obtaining accurate food habit data for golden eagles on the islands is critical to accurately assess the trophic interactions of this avian predator in the northern Channel Island ecosystem. The principal objectives of this study were to: (1) determine prey composition and abundance and dietary breadth of golden eagles nesting on the Channel Islands; (2) determine the importance of feral herbivores (piglets, sheep, mule deer fawns, and elk calves) and island foxes as prey for nesting golden eagles; and (3) document changes in the eagles' diet following the eradication of feral pigs from SCI.

STUDY AREA AND METHODS

Study Area

Santa Cruz and Santa Rosa islands, the two largest of the northern Channel Islands, are located approximately 30 km (19 mi) south and 44 km (27 mi) southwest, respectively, from the adjacent mainland. SCI lies about 9 km (5.5 mi) east of SRI and 7 km (4.5 mi) west of Anacapa Island. These two islands have a Mediterranean climate, with mild, wet winters and warm, dry summers. Most rain falls between November and April and averages about 50 cm (19.7 in) on SCI (Junak et al. 1995) and 30 cm (11.8 in) on SRI (Clark et al. 1990). Wind and fog are dominant climatic components on both islands. Strong northwest winds of 10 to 40 knots per hour drive moisture-laden marine air and summer fog across these islands. Diverse topography supports a total of 10 plant communities on SCI (Philbrick and Haller 1977) and 18 communities on SRI (Clark et al. 1990). Up to 89% of SCI is covered with grasslands, island chaparral, oak woodland, and coastal-sage and coyote-brush scrub (Minnich 1980), while 65% of SRI is covered with grasslands and 25% is covered with chaparral and six other scrub communities (Clark et al. 1990). Both of these islands contain a depauperate terrestrial bird and mammal fauna, with two medium-sized native mammals (island fox and western spotted skunk), several larger introduced herbivores (mule deer, elk, and feral pig), introduced California quail (*Callipepla californica*) and wild turkeys (*Meleagris* gallopavo; SCI only), and gopher snakes (*Pituophis catenifer*). Both islands also support large numbers of breeding and roosting cormorants, several other species of seabirds such as western gull (*Larus occidentalis*) and pigeon guillemot (*Cepphus columba*; Carter et al. 1992), and a diverse array of other migrant marine birds. Red-tailed hawks (*Buteo jamaicensis*) and common ravens (*Corvus corax*) are the largest land birds resident on the islands.

Nest Sites Excavated

Prey remains were collected from 11 golden eagle nests in 7 breeding territories on Santa Cruz (n =5 territories) and Santa Rosa (n=2) islands (Fig. 1). On SRI, the Trap Canyon territory contained one

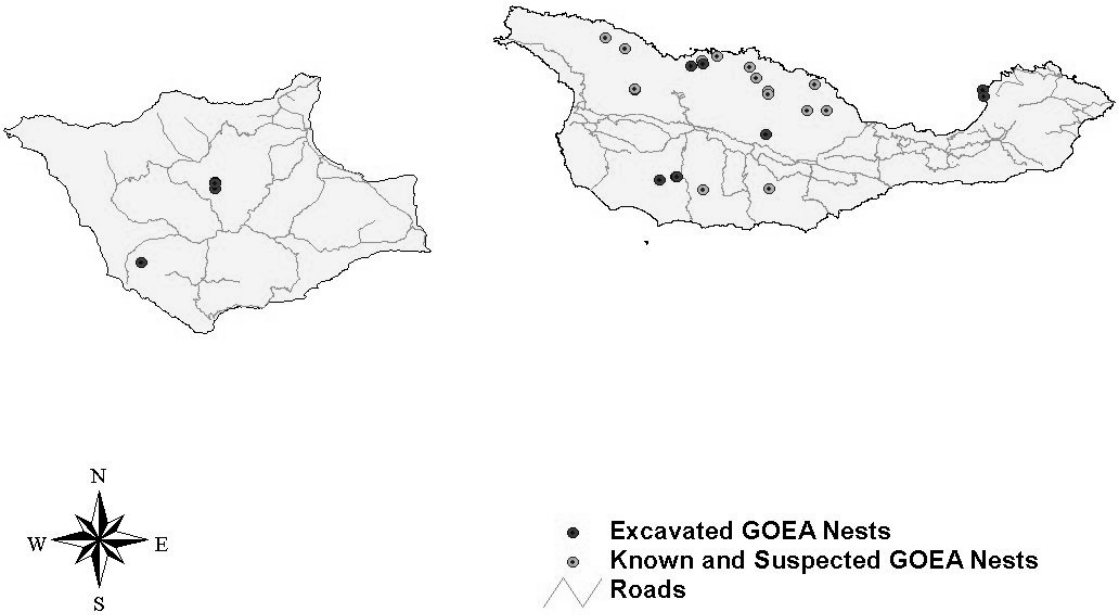

Figure 1. Golden eagle nests on Santa Cruz and Santa Rosa islands that were excavated for this study.

large nest (Big nest) and three smaller nests; while the Trancion Canyon territory contained one nest (Latta 2005). Based on the presence of multiple nest layers and/or multiple nests, the eagle territory in Trap Canyon was active from 1996 until 2004; while the Trancion Canyon territory was active from 2001 until 2003 (Latta 2005). On SCI there were at least five golden eagle nesting territories (i.e., Laguna Canyon, Cascada/Red Peaks, Coche Point, Lady's Harbor, and Christy Water Tank) with at least 29 large, eagle-sized nest structures (Fig. 1; Latta 2005). Based on the presence of multiple nest layers in the Laguna Canyon and two of the Coche Point nests, golden eagles have been nesting on SCI since at least the late 1980s or early 1990s. For this food habits study, one nest from the Trancion and three nests from the Trap Canyon territories on SRI, and two nests each from the Coche Point, Lady's Harbor, and Laguna Canyon territories and one nest from the Cascada territory on SCI were excavated. Only one (2006 nest) of the seven nests excavated on SCI for this food habits study was active following the eradication of feral pigs.

Sample Collection and Identification

Prey remains (bones and teeth) were collected from 11 golden eagle nests on Santa Cruz and Santa Rosa islands between 2002 and 2006. The surface and surrounding areas of each nest site were excavated by hand with prey remains collected and placed in bags labeled by the area within a nest site where the remains were found. After removing prey remains and loose material from the surface, successive layers of nest material were carefully excavated using trowels, shop brushes, and a 1/16-in. (1.59-mm) screen sieve. Remains recovered from each stratum were bagged according to nest layer (e.g., Layer A, B, C, etc.). Remains found outside the horizontal boundaries of the nest and not associated with a particular nest layer were placed in separate bags labeled by location found (e.g., back of nest ledge, below nest, etc.). Following excavation of each nest site, the stick nest structure was reconstructed using the original nest material (Latta et al. 2005).

Prey remains were first sorted into six taxonomic groups (bird, mammal, reptile, amphibian, fish, and invertebrates) and then identified in the lab to the highest taxonomic level possible by comparing diagnostic elements with identified specimens housed in research collections at the Santa Barbara Museum of Natural History. For mammals, a total of 16 elements (skull bones, mandible, teeth, scapula, humerus, radius, ulna, carpal/tarsal bones, metacarpals, pelvis, femur, tibia, fibula, calcaneus, astragalus, and metatarsal bones) were sufficiently diagnostic to permit identification to species. For birds, a total of 17 elements (crania, maxilla, lower mandible, pelvic bones, sternum, sacral vertebrae, humerus, ulna, radius, carpometacarpus, D4P=phalange of wing, coracoid, scapula, clavicle, femur, tibiotarsus, and tarsometatarsus) were used for species identifications. Bones not assignable to species (e.g., vertebrae, ribs, phalanges, and miscellaneous bone fragments) were listed as unidentified bird or mammal bone and were excluded from further identification or analysis. All diagnostic bird bones were identified to species except for bones from Brandt's and double-crested cormorants (*Phalacrocorax penicillatus* and *P. auritus*), and western and glaucous-winged gulls (*Larus occidentalis* and *L. glaucescens*). For these two species groups, their bones were too difficult to tell apart so they were lumped into these two species assemblages. Fish and invertebrate remains were considered to be incidental remains coming to the nest as crop or stomach contents of marine bird prey, as riders on materials used to line nest cups, or by being attracted to decomposing prey remains in nests. All incidental faunal remains were excluded from further quantitative diet analyses.

Data Analysis

Two measures were used to calculate diet composition. First, the minimum number of individuals (MNI) was determined for each species or species group to be equal to the greatest number of identical bone elements per taxon. Second, a body weight value (biomass) was assigned for each species identified in the prey samples by using published weight data for each taxon (see Appendix 2 in Collins and Latta 2006). Where sex of prey could not be determined, we averaged the means of each sex for weight estimates of individual species. For larger prey species, the weights of immature animals (e.g., newborns) of appropriate subspecies were also taken from the literature if available. For elk we used the weight at birth to one week of age (Johnson 1951), and for mule deer the weight at

birth (Anderson and Wallmo 1984). For sheep we used the weight recorded on SCI for lambs from birth to 6 months of age (Van Vuren and Coblentz 1984). For feral piglets, we used an estimate of 2.5 kg for the weight (e.g., birth to 1 month of age) which represents the average maximum weight of a prey item that an eagle could be expected to carry back to its nest (Huey 1962; Watson 1997). Although eagles undoubtedly fed on piglets, lambs, deer fawns, and elk calves that were older and too heavy to be carried back to their nests, it was impossible to determine an average weight for this type of prey. Thus, biomass estimates for these larger prey species are probably conservative.

Three analyses were conducted to determine diet composition. First, nests active on Santa Cruz and Santa Rosa islands were combined to examine diet composition for eagles on the islands prior to the removal of feral pigs from SCI. Second, diet composition was examined for each island separately using nests active prior to the removal of feral pigs. Finally, diet composition was examined for nests on SCI pre- and post-pig removal. Percent diet composition was examined relative to MNI and biomass. For MNI, percent diet composition was calculated as the minimum number of all prey items in a given taxonomic group, divided by the total minimum number of all prey items recovered, multiplied by 100. A similar method was used to calculate percent biomass using average body weights. Dietary breadth was calculated for both islands combined (exclusive of the 2006 Laguna Canyon nest on SCI) and separately for each island sample using Levins' (1968) formula: B=1/sum p_i^2 where p_i was the relative occurrence of prey i in the diet. Values of niche breadth range from 1 to n with 1 representing the narrowest value for food niche breadth.

RESULTS

Diet Composition—Combined Island Samples Pre-Pig Removal

We collected 4896 prey remains (i.e., bones, teeth, and otoliths) representing 27 prey species from 10 golden eagle nests active prior to the removal of feral pigs from the islands (6 nests on SCI and 4 nests on SRI, Table 1). Faunal remains from an 11th nest active following the removal of feral pigs on SCI were also collected but are analyzed separately and thus are not included in the following prey totals for the combined island samples. Of the 425 individuals identified, 222 (52.2% MNI) were birds, 195 (45.9%) were terrestrial mammals, and 8 (1.9%) were reptiles. Based on MNI, the three most important prey groups in this sample were introduced herbivores (26.8%), land birds (27.8%), and aquatic birds (24.5%), with all other prey classes combined accounting for 20.9% of the diet (Table 1).

The relative proportion of a prey category or species changed when prey biomass was used as the measure. The proportion of larger (heavier) species increased while smaller (lighter weight) species declined (Table 1). In terms of total biomass of prey recovered, terrestrial mammals and birds accounted for 59.5% and 40.3% of the eagles' overall nesting season diet, respectively, and reptiles comprised only 0.2% of the diet. By biomass, the most important species were feral piglets (31.4%), mule deer fawns (17.3%), common raven (17.4%), and island fox (7.2%; Table 1). While deer mice (*Peromyscus maniculatus*) comprised 9.6% of the eagles' diet based by MNI, they only comprised 0.13% of the eagles' diet based on biomass. Many other recorded prey also showed a decline when biomass was used as the measure (e.g., western spotted skunk, reptiles, land birds, and all marine birds except for cormorants).

Diet Composition—Separate Island Samples Pre-Pig Removal

There were island-specific differences in dietary breadth and composition of prey remains (Tables 2 and 3). Golden eagles on SRI had the most diverse diet (7.11 dietary breadth) with 19–20 species represented, while eagles on SCI had a less diverse diet (3.77) with 14–16 species represented. Species unique to SRI prey samples included waterfowl (mallard [*Anas platyrhynchos*] and gadwall [*Anas strepera*]), raptors (red-tailed hawk, peregrine falcon [*Falco peregrinus*], barn owl [*Tyto alba*]), loggerhead shrike (*Lanius ludovicianus*), 3 small passerine species, southern alligator lizard (*Elgaria multicarinata*), Santa Cruz gopher snake (*Pituophis catenifer pumilus*), mule deer fawns, and an elk calf (Table 2). Species unique to SCI prey

Table 1 . Diet of golden eagles nesting on Santa Cruz and Santa Rosa islands based on minimum number of individuals and on the biomass of individual prey species recovered from six nests on Santa Cruz Island and four nests on Santa Rosa Island.

				Biomass		
Common name	Scientific name	MNI[a]	%MNI[b]	Body weight (grams)	Total weight (grams)	Percent of total biomass
MAMMALS	MAMMALIA					
Deer mouse	*Peromyscus maniculatus*	41	9.6	20	820	0.13
Island fox	*Urocyon littoralis*	22	5.2	2036	44792	7.2
Western spotted skunk	*Spilogale gracilis amphiala*	18	4.2	560	10080	1.6
Feral pig	*Sus scrofa*	78	18.4	2500	195000	31.4
European mouflon sheep	*Ovis aries*	3	0.7	2300	6900	1.1
Mule deer	*Odocoileus hemionus*	32	7.5	3365	107680	17.3
Elk	*Cervus canadensis*	1	0.2	4500	4500	0.7
TOTAL MAMMALS		195	45.9		369772	59.5
BIRDS	AVES					
Double-crested/ Brandt's cormorant	*Phalacrocorax auritus/penicillatus*	23	5.4	1962	45126	7.3
Pelagic cormorant	*Phalacrocorax pelagicus*	10	2.4	1868	18680	3.0
Gadwall	*Anas strepera*	3	0.7	920	2760	0.4
Mallard	*Anas platyrhynchos*	21	4.9	1139	23919	3.8
Herring gull	*Larus argentatus*	2	0.5	1135	2270	0.4
California gull	*Larus californicus*	2	0.5	607	1214	0.2
Western/glaucous-winged gull	*Larus occidentalis/ glaucescens*	43	10.1	875	37625	6.1
Subtotal aquatic birds		104	24.5		131594	21.2
Red-tailed hawk	*Buteo jamaicensis*	1	0.2	1126	1126	0.2
American kestrel	*Falco sparverius*	1	0.2	116	116	tr[c]
Peregrine falcon	*Falco peregrinus*	1	0.2	768	768	0.1
California quail	*Callipepla californica*	5	1.2	173	865	0.14
Mourning dove	*Zenaida macroura*	1	0.2	127	127	tr
Barn owl	*Tyto alba*	14	3.3	524	7336	1.2
Loggerhead shrike	*Lanius ludovicianus*	1	0.2	47.4	47.4	tr
Common raven	*Corvus corax*	90	21.2	1199	107910	17.4
White-crowned sparrow	*Zonotrichia leucophrys*	1	0.2	25.5	25.5	tr

Table 1 (continued). Diet of golden eagles nesting on Santa Cruz and Santa Rosa islands based on minimum number of individuals and on the biomass of individual prey species recovered from six nests on Santa Cruz Island and four nests on Santa Rosa Island.

				Biomass		
Common name	Scientific name	MNI[a]	%MNI[b]	Body weight (grams)	Total weight (grams)	Percent of total biomass
Western meadowlark	*Sturnella neglecta*	2	0.5	100.7	201.4	tr
Brown-headed cowbird	*Molothrus ater*	1	0.2	43.9	43.9	tr
Subtotal land birds		118	27.8		118566.2	19.1
TOTAL BIRDS		222	52.2		250287	40.3
REPTILES	REPTILIA					
Southern alligator lizard	*Elgaria multicarinata*	5	1.2	50	250	tr
Santa Cruz gopher snake	*Pituophis catenifer pumilus*	3	0.7	520	1560	0.2
TOTAL REPTILES		8	1.9		1810	0.2
TOTAL PREY		425	100		621869	

a. MNI=minimum number of individuals.

b. Percentages are rounded to the nearest 0.1 of a decimal point and are based on all prey remains recovered.

c. tr = trace amount, < 0.05 percent.

samples included gulls (herring [*Larus argentatus*], California [*L. californicus*] and western/glaucous-winged gulls), American kestrel (*Falco sparverius*), California quail, feral piglets, and sheep (lambs and at least 1 adult; Table 3).

By biomass, terrestrial mammals accounted for 71.6% and 47.8% of the eagles' diet on Santa Cruz and Santa Rosa islands, respectively, while birds made up 28.3% and 51.6% (Tables 2 and 3). Mule deer fawns were the most important prey for eagles on SRI, comprising 34.6% of the prey biomass, while feral piglets were the most important prey for eagles on SCI, comprising 63.2%. On SRI the next most important prey were common raven (25.8%), cormorants (14.2%), waterfowl (8.6%), and island fox (8.5%); while on SCI the next most important prey were gulls (13.3%), common raven (8.9%), island fox (5.9%), and double-crested/Brandt's cormorant (5.7%).

Diet Composition 2006 Nest on SCI—Post-Pig Removal

regularly clean their nests by removing uneaten prey

Prey remains were also recovered from a single golden eagle nest that was active in spring 2006 after feral pigs had been eradicated from SCI. In compiling the prey remains from this nest site, there were problems determining the exact number of island foxes that were contained at the 2006 nest site as island fox carcasses, fox collars, and passive integrated transponder (PIT) tags were removed from the nest and areas surrounding the nest by biologists from the Institute for Wildlife Studies (IWS) prior to our 2007 excavation of this nest site. As not all of the foxes represented in the nest were marked, we were unable to clarify the exact number of island foxes that were associated with the recovered carcasses, collars, and tags. As a result, we have provided in the following dietary analysis for the 2006 nest site an upper (n=14 foxes) and lower (n=12) limit for the number of island foxes that are believed to have been associated with this nest site. The actual number of island foxes eaten by the pair of eagles that used the Laguna nest in 2006 is probably more than 14 foxes since eagles (Watson 1997).

Table 2. Nesting season diet of golden eagles on Santa Rosa Island based on prey remains from four nests (two territories).

Common name	Scientific name	MNI[a]	Percent MNI[b]	Species weight (grams)	Percent of total
MAMMALS	MAMMALIA				
Deer mouse	*Peromyscus maniculatus*	36	14.9	20	0.2
Island fox	*Urocyon littoralis*	13	5.4	2036	8.5
Western spotted skunk	*Spilogale gracilis amphiala*	17	7	560	3.1
Mule deer	*Odocoileus hemionus*	32	13.2	3365	34.6
Elk	*Cervus canadensis*	1	0.4	4500	1.4
TOTAL MAMMALS		99	40.9		47.8
BIRDS	AVES				
Double-crested/Brandt's cormorant	*Phalacrocorax auritus/penicillatus*	13	5.4	1962	8.2
Pelagic cormorant	*Phalacrocorax pelagicus*	10	4.1	1868	6.0
Gadwall	*Anas strepera*	3	1.2	920	0.9
Mallard	*Anas platyrhynchos*	21	8.7	1139	7.7
Subtotal aquatic birds		47	19.4		22.8
Red-tailed hawk	*Buteo jamaicensis*	1	0.4	1126	0.4
Peregrine falcon	*Falco peregrinus*	1	0.4	768	0.2
Barn owl	*Tyto alba*	14	5.9	524	2.4
Loggerhead shrike	*Lanius ludovicianus*	1	0.4	47.4	tr[c]
Common raven	*Corvus corax*	67	27.7	1199	25.8
White-crowned sparrow	*Zonotrichia leucophrys*	1	0.4	25.5	tr
Western meadowlark	*Sturnella neglecta*	2	0.8	100.7	0.1
Brown-headed cowbird	*Molothrus ater*	1	0.4	43.9	tr
Subtotal land birds		88	36.4		28.9
TOTAL BIRDS		135	55.8		51.6
REPTILES	REPTILIA				
Southern alligator lizard	*Elgaria multicarinata*	5	2.1	50	0.1
Santa Cruz gopher snake	*Pituophis catenifer pumilus*	3	1.2	520	0.5
TOTAL REPTILES		8	3.3		0.6
TOTAL PREY		242	100		100

a. MNI=minimum number of individuals.

b. Percentages are rounded to the nearest 0.1 of a decimal point and are based on all prey remains recovered.

c. tr = trace amount, < 0.05 percent.

Table 3. Diet of golden eagles nesting on Santa Cruz Island before feral pigs were eradicated (six nests) and after pigs were eradicated (one nest).

	Nests active pre-pig eradication (n = 6)				Nests active post-pig eradication (n = 1)		
Common name	MNI[a]	Percent MNI[b]	Species weight	Percent biomass[b]	MNI[a]	Percent MNI[b]	Percent biomass[b]
MAMMALS							
Deer mouse	4	2.2	20	tr[c]			
Island fox	9	5.0	2036	5.9	12–14	30.8–37.8	45.7–57.7
Western spotted skunk	1	0.6	560	0.18			
Feral pig	78	43.1	2500	63.2			
European mouflon sheep	3	1.7	2300	2.2			
TOTAL MAMMALS	95	52.5		71.6	12–14	30.8–37.8	45.7–57.7
BIRDS							
Double-crested/Brandt's cormorant	9	5.0	1962	5.7			
Pelagic cormorant			1868		1	2.6–2.7	3.5–3.8
Herring gull	2	1.1	1135	0.74			
California gull	2	1.1	607	0.39			
Western/glaucous-winged gull	43	23.8	875	12.2	11	28.2–29.7	18.0–19.5
Subtotal aquatic birds	56	30.9	2743	19.0	12	30.8–32.4	21.5–23.3
American kestrel	1	0.6	116	0.04	1	2.6–2.7	0.22–0.23
California quail	5	2.8	173	0.28	1	2.6–2.7	0.32–0.35
Mourning dove	1	0.6	127	tr			
Common raven	23	12.7	1199	8.9	11	28.2–29.7	24.7–26.7
Subtotal land birds	30	16.6		9.3	13	33.3–35.1	25.0–27.3
TOTAL BIRDS	86	47.5		28.3	25	64.1–67.6	46.7–50.6
TOTAL PREY	181	100			37–39	100	100

a. MNI=minimum number of individuals.

b. Percentages are rounded to the nearest 0.1 of a decimal point and are based on all prey remains recovered.

c. tr = trace amount, <0.05 percent.

A total of 37–39 individuals were recovered from the 2006 nest with birds comprising 46.7–50.6% and land mammals comprising 45.7–57.7% of the recovered prey biomass (Table 3). In the absence of feral piglets, the Laguna pair of golden eagles preyed more intensively on island foxes (45.7–57.7%), common ravens (24.7–26.7%), and gulls (18.0–19.5%). Island foxes and common ravens went from comprising 5.9% and 8.9% of the eagle's prey biomass prior to the removal of pigs to comprising 45.7–57.7% and 24.7–26.7% of the prey biomass following the removal of feral pigs (Table 3).

DISCUSSION

Diet Composition

The nesting season diet of golden eagles on the Channel Islands differed from diets recorded from 18 other golden eagle food habit studies in North America (see Appendix 1 in Collins and Latta 2006). On the islands, golden eagles fed more intensively on birds (52.2% MNI) than the average (20.5%) recorded from published eagle food habit studies in North America. Also, land mammals comprised a smaller percentage of the eagles' diet on the islands (45.9%) than the 76.7% average recorded from 18 eagle food habit studies in North America. The absence of an abundant diurnally active native mammal or avian prey, like that found elsewhere in North America (e.g., Sciurids, Leporids, and Gallinaceous birds), contributed to golden eagles on the Channel Islands switching to other prey less frequently eaten by eagles, such as feral piglets, mule deer fawns, common raven, island fox, spotted skunk, gulls, waterfowl, cormorants, and barn owls. Golden eagles on the islands have adapted their foraging strategies to access and harvest diurnally active terrestrial and aquatic vertebrate prey found on the islands. This switch to alternative prey has had a dramatic adverse effect on the endemic island fox that had evolved in the absence of a large terrestrial avian predator like the golden eagle.

Golden eagles are adept predators of birds as evidenced by the diversity of species eaten and the relative importance of birds (3.9% to 47.6% MNI) in golden eagle diets elsewhere in North America (Arnell 1971; Olendorff 1976; Marr and Knight 1983). On the Channel Islands, birds comprised 52.2% (MNI) of the prey remains which represents the highest percentage for birds recorded in the diet of any golden eagle population in North America. While gallinaceous birds are an important secondary prey for golden eagles in some areas of North America, Scotland, and continental Europe and Asia (Watson 1997; Kochert et al. 2002), they were scarce in the eagles' diet on the Channel Islands. The only gallinaceous birds available to eagles on the islands were introduced California quail (both islands) and wild turkeys (SCI only). Both species tend to inhabit more heavily wooded habitats on the islands making them less visible and thus less accessible to foraging eagles. California quail were only taken by eagles a few times and as such were a relatively unimportant prey constituent (1.2% MNI) in the eagles' diet on the islands. Common ravens and cormorants were the most important avian prey for eagles on the Channel Islands. These two species comprised 17.4% and 10.2% of the prey biomass consumed by eagles on the islands, and both species are rare in eagle diets elsewhere in North America and Europe (Olendorff 1976; USDI 1979; Eakle and Grubb 1986; Watson 1997). Waterfowl, gulls, and barn owls were also important prey for eagles on the islands but have only occasionally been eaten by eagles elsewhere in the world (Carnie 1954; Olendorff 1976; USDI 1979; Bloom and Hawks 1982; Collopy 1983; Watson 1997). Clearly, in the absence of an abundant diurnally active terrestrial prey, golden eagles on the Channel Islands have developed foraging strategies to catch alternative avian prey that are uncommon to rare in eagle diets elsewhere in North America. While most avian bones found in eagle nests on the islands were from subadult and adult birds, there were some juvenile/nestling bones of cormorants, gulls, common ravens, and barn owls. The presence of nestling bone from these species suggests that golden eagles on the islands were occasionally capturing young birds by nest robbing.

Of 7094 prey remains identified in golden eagle nests in North America, hoofed mammals and domestic livestock remains accounted for 1.4% and 4.4% (MNI) of the remains, respectively (Olendorff 1976). In North America mule deer comprised 0.1% and 12.7% of the eagles' nesting season diet (Watson 1997). Feral herbivores were an even more important prey constituent of the eagles' diet on the islands with feral pigs comprising 43.1% MNI (63.2% biomass) on SCI and mule deer fawns comprising 13.2% MNI (34.6% biomass) on SRI. All of the feral pig and mule deer bones found in eagle nests on the islands were from very young animals (piglets and fawns) which are within the eagles' preferred, transportable prey size (0.5–4.0 kg). Feral pigs have been reported in only 6 of 24 golden eagle food habit studies from continental Europe and Asia where they comprised 0.3% to 2.7% MNI of the eagles' diet (Watson 1997). As a result of the depauperate nature of terrestrial vertebrate prey on SCI, eagles have increased their reliance on feral pigs (43.1% MNI). This is due to

the abundance and seasonal availability of feral piglets during the eagles' spring breeding season, and because piglets (0–2 months of age) are within the eagles' preferred prey size. Given the number of eagle nesting territories on SCI (n=5), it is clear that feral pigs were probably the principal reason why eagles were able to successfully establish and maintain a breeding presence on the northern Channel Islands. Mule deer fawns probably played a similar role in helping eagles to establish a breeding presence on SRI. The ongoing occurrence of mule deer and elk on SRI will continue to attract eagles to this island and could lead to eagles attempting to nest again on this island.

Carnivores are typically only incidental prey for golden eagles, with most occurrences resulting from eagles scavenging on carcasses rather than actively preying on live animals. Carnivores comprised less than 1.0% of golden eagles' overall diet in North American food habit studies (Olendorff 1976). However, in several studies carnivores comprised a higher percentage of an eagles' diet, such as 5.4% of the overall diet in one study in California (Carnie 1954) and 13.2% of the eagles' diet in another study in Arizona (Eakle and Grubb 1986). Until the present study, the highest representation of carnivores in a golden eagle diet was in Mongolia, where carnivores comprised 41% MNI of the total prey remains recovered from an excavated nest (Ellis et al. 1999). On the Channel Islands, carnivores (island fox and western spotted skunk) comprised 9.4% MNI of the eagles' overall diet on both islands and 5.6% of the eagles' diet on SCI prior to the eradication of feral pigs. Following the removal of pigs from SCI, island fox increased to 30.6–37.8% MNI (45.7–57.7% biomass) at the only active eagle nest on the island. This represents one of the highest percentages ever recorded for carnivores in the diet of a golden eagle population. Spotted skunks made up 7.0% MNI and 0.6% MNI of the eagles' diet on Santa Rosa and Santa Cruz islands, respectively, and represent the first time that this species has been documented being eaten by golden eagles. On the Channel Islands eagles are feeding more intensively on terrestrial carnivores due in part to (1) the depauperate nature of diurnally active terrestrial vertebrate prey on the islands, (2) the fact that both species are within the eagles' preferred prey size, and (3) both carnivores exhibiting some diurnal activity which makes them accessible to foraging eagles. Predation from golden eagles clearly has had a significant adverse effect on island fox populations on three of the northern Channel Islands (Roemer et al. 2001, 2002; Coonan et al. 2002) and will continue to impact these populations into the future if any eagles remain as year-round residents on Santa Cruz or Santa Rosa islands.

Diet Composition—Post-Pig Eradication

Based on prey remains recovered from the only golden eagle nest which was active after feral pigs were eradicated from SCI (Laguna 2006 nest), this pair of eagles was able to switch from preying intensively on feral piglets to preying more intensively on island foxes, western gulls, and common ravens. Between July 2005 and June 2006, the Laguna pair of eagles is believed to have been responsible for more than 20 island fox mortalities (Schmidt et al. 2007). The implications of these results are that if golden eagles remain as residents on the northern Channel Islands, they will continue to adversely impact island fox populations through selective predation of this species, a fact which seems to be supported by ongoing eagle-fox related mortalities on SCI following the removal of the Laguna Canyon pair of eagles (Morrison 2007) and by recent eagle-fox mortalities on SRI (T. Coonan, personal communication). Without feral piglets to feed on, eagles are preying on the next similar-sized terrestrial prey, the island fox. The impact of this predation to fox populations on the islands will depend on the number of eagles that remain on the islands and on whether these eagles attempt to breed and rear young on the islands.

Dietary Breadth

Dietary breadth is the best measure of how specialized an eagle's diet is. In North America, eagles show a dependence on just one or two prey families (Leporidae or Sciuridae), which has led to an average dietary breadth measured from 13 food habits studies of 2.74 (range 1.36–5.36; Watson 1997). In Europe and Asia, the average dietary breadth measured from 24 golden eagle food habit studies was 4.03 (range 2.01–11.2) and from 9 food habit studies in Scotland was 5.38 (2.44–7.25; Watson 1997). Dietary breadth in Scotland, Europe, and Asia was higher than that recorded in North America because golden eagles preferred prey from

two, three, or four of the principal prey families (Leporidae, Sciuridae, Tetraonidae, and Phasianidae; Watson 1997).

Golden eagles usually exhibit a more diverse diet when their preferred prey is scarce or absent. On the Channel Islands, where rabbits, squirrels, and larger-sized Gallinaceous birds are absent, golden eagles have developed a more diverse diet (average dietary breadth 8.63) than elsewhere in North America (average dietary breadth 2.74). Eagles on the islands have broadened their diet to include a wider diversity of prey, including a number of species that eagles are not known to feed on intensively, such as feral pigs, common raven, island fox, western spotted skunk, cormorants, gulls, waterfowl, and barn owls. Because of their heavier reliance on feral piglets (63.2% of prey biomass), eagles on SCI exhibit a more specialized diet (3.77 dietary breadth) than eagles on SRI (7.11). Following the removal of pigs from SCI, eagles shifted to feeding more intensively on three species (island fox, common raven, and gulls) which resulted in a slightly higher dietary breadth of 3.86. Golden eagle populations on islands off Scotland exhibited moderately diverse diets (3.47–5.14) comprised of three or four dominant prey families (Watson 1997). Eagles on two islands in Europe have exhibited very narrow diets comprised of unusual prey species. On the island of Gotland in Sweden, where rabbits are rare, eagles have shifted to preying more intensively on hedgehogs (Hogstrom and Wiss 1992); while on the island of Macedonia their principal prey is tortoises (Grubac 1987). Eagles on these two islands shifted to utilizing unusual prey species because both species fall within golden eagles' preferred size range for prey and both species were available in sufficient quantity (Watson 1997). This is probably also the same reason why golden eagles on the Channel Islands have shifted to preying on species that are not normally eaten by eagles elsewhere in North America.

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REPRODUCTIVE PERFORMANCE OF ASHY STORM-PETRELS (*OCEANODROMA HOMOCHROA*) AT SANTA CRUZ ISLAND, CALIFORNIA, IN 1995–2007

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Abstract—In 1995–1998 and 2005–2007, reproductive performance of the ashy storm-petrel (*Oceanodroma homochroa*) was measured at four sea caves and one offshore rock at Santa Cruz Island, California. In 1995–1998, relatively low hatching success (62.2%) occurred, with broken eggs accounting for 53% of failed eggs, consistent with documented eggshell thinning from organochlorine pollutants. Hatching success was higher in 2005–2007 (72.6%), with fewer broken eggs (32.7%), reflecting reduced pollutant levels, lower predation, and other factors. Fledging success was high in 1995–1998 (91.7%) and 2005–2007 (86.5%). Breeding success was moderate in 1995–1998 (54.9%) and 2005–2007 (63.4%). Predation by barn owls (*Tyto alba*) was prominent in 1995–1998 but not in 2005–2007. In 2005, island spotted skunks (*Spilogale gracilis amphiala*) killed at least 76 adults and caused complete reproductive failure at Bat Cave. By 2007, numbers of nests at Bat Cave had returned to about 40% of pre-2005 levels. Differences in reproductive performance between locations at Santa Cruz Island apparently were related to predation, human disturbance, and bright lights from squid-fishing boats.

INTRODUCTION

The ashy storm-petrel (*Oceanodroma homochroa*) is globally rare with a restricted breeding distribution on islands and islets off central and southern California, USA, and northwest Baja California, Mexico (Ainley 1995; Carter et al. 2008a). Largest colonies occur on the South Farallon Islands off central California; and on San Miguel, Santa Barbara, and Santa Cruz islands in the Channel Islands off southern California (Sowls et al. 1980; Ainley et al. 1990; Carter et al. 1992). World population size has been estimated at about 10,000 individuals (Sowls et al. 1980; Ainley 1995). Many aspects of reproductive biology are reasonably well known. Adults do not excavate burrows; rather, they nest in crevices of talus slopes, rock walls, sea caves, cliffs, and driftwood (James-Veitch 1970; Ainley et al. 1990; McIver 2002). The breeding season is protracted, and breeding activities (courtship, incubation, chick-rearing) at nesting locations can occur throughout the year (James-Veitch 1970; Ainley et al. 1974). The egg-laying period extends from late April to October, peaking in June and July (James-Veitch 1970; Ainley et al. 1990; McIver 2002). Clutch size is one egg, and parents alternate incubation bouts during an average incubation period of about 44 days (James-Veitch 1970; Ainley 1995). Some pairs will lay replacement eggs after failure of a first egg (Ainley et al. 1990; McIver 2002). Nestlings are brooded for about five days, and then chicks are left alone in the nest site (except during parental feedings every 1 to 3 nights on average) until they fledge when about 66 to 85 days old (James-Veitch 1970; Ainley et al. 1990). Peak fledging occurs in

early to mid-October but latest chicks can fledge in January in some years (Ainley et al. 1990; McIver 2002). Nocturnal visits to crevice breeding sites reduce predation by diurnal predators such as western gulls (*Larus occidentalis*) and peregrine falcons (*Falco peregrinus*), although adults are preyed upon at night by burrowing owls (*Athene cunicularia*) and barn owls (*Tyto alba*) (Ainley 1995; McIver 2002). Island spotted skunks (*Spilogale gracilis amphiala*) are the only known mammalian predators of adult ashy storm-petrels, although eggs and small chicks are eaten or scavenged by house mice (*Mus musculus*) and deer mice (*Peromyscus maniculatus*) on occasion (Ainley et al. 1990; McIver 2002; McIver and Carter 2006).

Most published research on the reproductive biology of this species has been limited to Southeast Farallon Island (37°42'N, 123°00'W; hereafter SEFI), located in the northern part of the breeding range in the central portion of the California Current, where several studies and annual nest monitoring have been conducted since 1965 (James-Veitch 1970; Ainley et al. 1974, 1976, 1990; Sydeman et al. 1998b). In 1995–1998, Humboldt State University and collaborators studied reproductive biology of ashy storm-petrels at Santa Cruz Island (centered at about 34ºN latitude and between 119º40' and 119º50'W longitude; hereafter SCI) to investigate possible differences in breeding biology in the southern part of the breeding range in the Channel Islands within the southern portion of the California Current (McIver 2002). In 2005–2007, U.S. Fish and Wildlife Service and collaborators continued studies of reproductive biology, mainly to provide further recent baseline data for restoration efforts at SCI which began in 2008 (McIver and Carter 2006; Carter et al. 2007; McIver et al. 2008, 2009). In this paper, reproductive performance of ashy storm-petrels at SCI in 1995–2007 is summarized and potential impacts of pollutants, predators, and other factors are discussed. Due to space limitations and analysis difficulties, statistical comparisons of reproductive performance (between SCI locations and years, and between SCI and SEFI), SCI population trends, effects of pollutants, and restoration efforts at SCI will be covered in other papers.

METHODS

SCI is located approximately 40 km south of Santa Barbara, within Santa Barbara County, California, and is the largest (249 km^2) of the eight major Channel Islands (Minnich 1980). SCI is jointly managed by the Nature Conservancy (central and west parts) and the National Park Service (NPS; east end). The north coast of the island is composed largely of sheer cliffs and bluffs, with at least 110 sea caves at the base of these cliffs (Bunnell 1988). Ashy storm-petrels have been found breeding at 11 locations at SCI, including sea caves and offshore rocks (Carter et al. 2008a). In 1995–1998 and 2005–2007, reproductive performance of ashy storm-petrels was examined at four sea caves and one offshore rock along the north coast of SCI. Sea caves ranged from about 15 to 100 m in depth, with floors free of spray or standing water throughout most of the year. Cave of the Bird's Eggs (CBE) and Dry Sandy Beach Cave (DSB) were located on the remote northwest shore, while Cavern Point Cove Caves (CPC) and Bat Cave (BC) were located on the more accessible northeast shore. In these sea caves, ashy storm-petrels nested in crevices within rock piles, along the edges of cave walls, and (BC only) in driftwood piles. In addition, storm-petrels nested on occasion in open floor depressions adjacent to cave walls. At Orizaba Rock (OR), a small islet ~100 m offshore of the north central coast of SCI, storm-petrels nested in crevices occurring in rock walls, under rocks, and in floors of small caverns. These five locations were selected for this study because each location was accessible using a small inflatable boat powered by an outboard engine under most weather conditions and an adequate sample size of nests was available at each location to assess reproductive performance. In 1995–1997 and 2005, all five locations were studied. In 1998, only CBE and DSB were examined (due to lower funding) to detect any effects from intense El Niño conditions. In 1999–2003, reproductive performance was not studied due to a lack of funding, although single trips per year were made to assess changes in population size. No data were collected in 2004. In 2006–2007, only CPC, BC, OR, and CBE were included in baseline data gathered for restoration work; DSB was excluded because it was furthest from restoration sites and was the most difficult location to access and study.

To determine reproductive performance at a SCI location in each study year, all accessible habitats at each location were searched with small flashlights for active nests (i.e., with incubating adults, whole eggs, or fresh eggshell fragments) every 3–5 weeks, usually monthly, from May–June to October–November. Active nests were tagged, then checked on subsequent visits using flashlights from a distance of 0.5 to 3.0 m to briefly view nest contents. When briefly illuminated, adults usually would lift up enough to expose the egg. However, if not, adults were lightly prodded with a 30 cm wooden dowel in accessible nest sites to confirm egg presence. On each visit, nest status and chick development were recorded. In several storm-petrel studies, researcher disturbance has been demonstrated to reduce breeding success, with lower hatching success resulting from nest desertion (James-Veitch 1970; Boersma et al. 1980; Ainley et al. 1990; Blackmer et al. 2004). Researcher disturbance was minimized through infrequent nest checks every 3–5 weeks during incubation and chick periods (also necessitated by limited funds for staff and charter boats to visit these remote SCI locations), brief location visits that lasted 1–4 hours, non-handling of adults in nests, avoiding impacts to incubating adults from noise or lights, and avoiding impacts to fragile nesting habitats from trampling. To evaluate breakage of eggs and predation eggshell fragments, feather piles, carcasses, and avian pellets were collected when found to prevent double counting. Unattended eggs were left in nest sites for 2–3 months before being considered abandoned and being removed.

Within a nesting season, if only one egg was laid in a nest site, it was categorized as a "single" egg. If two eggs were found in a nest site (where a first egg had been laid but failed), the first egg was categorized as "first" and the second egg was considered a "replacement" egg presumably laid by the same breeding pair. Fates of eggs were categorized as hatched, broken, whole and did not hatch, missing, or unknown. To assess fledging with infrequent nest checks, chick ages were estimated on the basis of estimated egg laying and hatching dates, and plumage development. In almost all cases, a missing chick was assumed to have fledged, if last seen as fairly large and apparently healthy or > 66 days of age (minimum age of fledging; James-Veitch 1970). Hatching success for an SCI location was estimated as the percentage of single and first eggs (combined) that hatched; replacement eggs were excluded from this calculation because they were not independent of first eggs and would have contributed more than one value for certain nest sites. Fledging success for an SCI location was estimated as the percentage of chicks fledged out of those hatched from single, first, and replacement eggs. Breeding success for an SCI location was estimated as the percentage of chicks that fledged per breeding pair (from eggs that were either single or replacement eggs). For general description of reproductive performance in this paper, average SCI values were calculated for hatching, fledging, and breeding success per year and for periods of years by combining all nest sites studied. However, these average values did not account for variation in locations studied per year, differences in annual sample sizes studied, and differences in success between locations within and between years. These issues potentially affected statistical analyses, and this paper focuses on summarizing information obtained rather than examining statistical differences, which will be addressed in future papers.

RESULTS

Hatching, Fledging, and Breeding Success

Totals of 749 single/first clutches and 30 replacement clutches were documented at SCI in 1995–2007 (Table 1). Largest samples of single/first clutches were found in BC (n = 278 in 5 years) and DSB (n = 196 in 5 years), with lower samples in CBE (n = 107 in 7 years), OR (n = 91 in 6 years), and CPC (n = 77 in 6 years). Only 8 single/first clutches and no replacement clutches had unknown fates.

Hatching success at SCI averaged 62.2% in 1995–1998 and 72.6% in 2005–2007 (Table 2). Average hatching success in 1995–2007 was lowest at OR and CPC (54.9% and 55.1%, respectively) and highest at DSB and CBE (73.7% and 74.8%, respectively; Table 2). Fledging success at SCI averaged 91.7% in 1995–1997 and 86.5% in 2005–2007 (Table 3). Average fledging success in 1995–2007 was lowest at CPC (84.6%) and highest at DSB (92.4%; Table 3). Breeding success at SCI averaged 54.9% in 1995–1998 and 63.4% in 2005–2007 (Table 4). Average breeding success in 1995–

Table 1. Numbers of ashy storm-petrel eggs monitored for reproductive performance at five locations on Santa Cruz Island, California, in 1995–2007. Codes: Clutch (1, first or single eggs; 2, replacement eggs, unknown fates in parentheses); and ND (no data). Locations are: Bat Cave (BC), Cave of the Bird's Eggs (CBE), Cavern Point Cove Caves (CPC), Dry Sandy Beach Cave (DSB), and Orizaba Rock (OR).

		Year									
Location	Clutch	1995	1996	1997	1998	2005	2006	2007	1995–1998	2005–2007	1995–2007
BC	1	64 (2)	97	70 (1)	ND	ND	19	28	231 (3)	47	278 (3)
	2	4	4	2	ND	ND	0	4	10	4	14
CBE	1	13	11	8 (1)	9	19	20	27	41 (1)	66	107 (1)
	2	1	0	0	0	2	1	1	1	4	5
CPC	1	16	11	17	ND	13	7	14	44	33	77
	2	0	2	2	ND	0	0	0	4	0	4
DSB	1	26	41	46	42	43	ND	ND	155	41	196
	2	1	2	0	0	0	ND	ND	3	0	3
OR	1	20	27	8	ND	7	15	14	55	36	91
	2	2	2	0	ND	0	0	0	4	0	4
Total	1	139 (2)	187	149 (2)	51	79	61	83	526	223	749 (4)
	2	8	10	4	0	2	1	5	22	8	30

2007 was lowest at CPC (44.4%) and highest at DSB (67.0%; Table 4).

In 1995–2007, broken and missing eggs accounted for 44.2% and 34.7% of 282 eggs that failed to hatch (Table 5). Most (76.2%) eggs that did not hatch were observed in the 1995–1998 period (Table 5).

Predation

In 1995–1997, 83 storm-petrel carcasses killed by avian predators were documented at SCI, including 76 adults and 7 chicks. Most (90.4%) were found at BC below at least two perches used by barn owls and one barn owl was observed in 1996. At OR, barn owls were observed and heard at night

Table 2. Hatching success (percentage) of ashy storm-petrels at five locations on Santa Cruz Island, California, in 1995–2007. Sample sizes in parentheses. Codes in Table 1.

	Year									
Location	1995	1996	1997	1998	2005	2006	2007	1995–1998	2005–2007	1995–2007
BC	56.3 (64)	59.8 (97)	60.0 (70)	ND	ND	89.5 (19)	67.9 (28)	58.9 (241)	76.6 (47)	61.9 (278)
CBE	61.5 (13)	81.8 (11)	75.0 (8)	88.9 (9)	63.2 (19)	70.0 (20)	85.2 (27)	75.6 (41)	74.2 (66)	74.8 (107)
CPC	31.3 (16)	18.2 (11)	52.9 (17)	ND	76.9 (13)	100 (7)	71.4 (14)	36.4 (44)	79.4 (33)	55.1 (77)
DSB	76.9 (26)	58.5 (41)	87.0 (46)	83.3 (42)	62.8 (43)	ND	ND	76.8 (155)	62.8 (41)	73.7 (196)
OR	70.0 (20)	25.9 (27)	50.0 (8)	ND	85.7 (7)	80.0 (15)	50.0 (14)	45.5 (55)	69.4 (36)	54.9 (91)
Total	59.7 (139)	53.5 (187)	67.8 (149)	84.3 (51)	67.1 (79)	82.0 (61)	71.1 (83)	62.2 (526)	72.6 (223)	65.6 (749)

Table 3. Fledging success (percentage) of ashy storm-petrels at five locations on Santa Cruz Island, California, in 1995–2007. Sample sizes in parentheses. Codes in Table 1.

	Year									
Location	1995	1996	1997	1998	2005	2006	2007	1995–1998	2005–2007	1995–2007
BC	96.9 (32)	86.0 (50)	97.4 (38)	ND	ND	75.0 (16)	94.7 (19)	92.5 (120)	85.7 (35)	91.0 (155)
CBE	100 (6)	100 (8)	80.0 (5)	80.0 (5)	76.9 (13)	91.7 (12)	87.0 (23)	91.7 (24)	85.4 (48)	87.5 (72)
CPC	75.0 (4)	66.7 (3)	100 (7)	ND	80.0 (10)	100 (6)	77.8 (9)	85.7 (14)	84.0 (25)	84.6 (39)
DSB	94.7 (19)	95.2 (21)	100 (36)	78.8 (33)	95.7 (23)	ND	ND	91.7 (109)	95.7 (23)	92.4 (132)
OR	90.9 (11)	85.7 (7)	100 (3)	ND	66.7 (6)	83.3 (12)	100 (7)	90.5 (21)	84.0 (25)	87.0 (46)
Total	94.4 (72)	88.8 (89)	97.8 (89)	78.9 (38)	84.6 (52)	84.8 (46)	89.7 (58)	91.7 (288)	86.5 (156)	89.9 (444)

on several occasions during mist-netting efforts in 1995–1996 (H.R. Carter, unpublished data). In 1995–1997, owl pellets collected at BC (n = 9) and OR (n = 4) contained remains (feathers, bones) of adult ashy storm-petrels (n = 9), downy storm-petrel chicks (n = 2), and deer mice (dentary bones, hair; n = 2). Only eight feather piles were detected at CBE (2006: n = 2; 2007: n = 3), CPC (2005: n = 1; 2007: n =1), and DSB (2005: n = 1). No evidence of avian predation of storm-petrels was detected at BC or OR in 2005–2007.

In 1995–2007, no evidence of predation of storm-petrels by western gull (e.g., gull pellets or observations of gulls inside caves) was detected at SCI. About seven gull nests were documented per year at OR, and gulls were observed flying near entrances to sea caves on several occasions. Common ravens (*Corvus corax*) were observed at the entrances of all caves on several occasions. In 1997, a raven was observed inside CBE and a dead pigeon guillemot (*Cepphus columba*) chick apparently had been recently killed by ravens. Eight and one pigeon guillemot carcasses were found at

Table 4. Breeding success (percentage) of ashy storm-petrels at five locations on Santa Cruz Island, California, in 1995–2007. Sample sizes in parentheses. Codes in Table 1.

	Year									
Location	1995	1996	1997	1998	2005	2006	2007	1995–1998	2005–2007	1995–2007
BC	52.5 (59)	48.9 (88)	58.7 (63)	ND	ND	66.7 (18)	66.7 (27)	52.9 (210)	66.7 (45)	55.3 (255)
CBE	54.5 (11)	80.0 (10)	57.1 (7)	66.7 (6)	55.6 (18)	61.1 (18)	74.1 (27)	64.7 (34)	65.1 (63)	64.9 (97)
CPC	20.0 (15)	10.0 (10)	46.7 (15)	ND	61.5 (13)	100 (6)	53.8 (13)	27.5 (40)	65.6 (32)	44.4 (72)
DSB	75.0 (24)	52.6 (38)	85.7 (42)	65.0 (40)	57.9 (38)	ND	ND	69.4 (144)	57.9 (38)	67.0 (182)
OR	60.0 (15)	22.2 (27)	42.9 (7)	ND	57.1 (7)	66.7 (15)	53.8 (13)	36.7 (49)	60.0 (35)	46.4 (84)
Total	54.0 (124)	45.1 (173)	64.9 (134)	65.2 (46)	57.9 (76)	68.4 (57)	65.0 (80)	54.9 (477)	63.4 (213)	57.5 (690)

Table 5. Fates of unsuccessful ashy storm-petrel eggs (percentage of failed single, first, and second clutches combined) at five locations at Santa Cruz Island, California, in 1995–2007. Fates are coded: broken (B), whole but did not hatch (DNH), and missing (M). Sample sizes in parentheses. Other codes in Table 1.

		Year									
Location	Failed egg fate	1995	1996	1997	1998	2005	2006	2007	1995–1998	2005–2007	1995–2007
BC	B	74.2 (23)	54.8 (23)	48.3 (14)	ND	ND	100 (2)	8.3 (1)	59.1 (60)	54.2 (3)	57.1 (63)
	DNH	0 (0)	4.8 (2)	41.4 (12)	ND	ND	0 (0)	83.3 (10)	15.4 (14)	41.7 (10)	25.9 (24)
	M	25.8 (8)	40.5 (17)	10.3 (3)	ND	ND	0 (0)	8.3 (1)	25.5 (28)	4.2 (1)	17.0 (29)
CBE	B	16.7 (1)	50.0 (1)	0 (0)	100 (1)	0 (0)	42.9 (3)	60.0 (3)	41.7 (3)	34.3 (6)	38.5 (9)
	DNH	16.7 (1)	0 (0)	50.0 (1)	0 (0)	57.1 (4)	42.9 (3)	0 (0)	16.7 (2)	33.3 (7)	23.8 (9)
	M	66.7 (4)	50.0 (1)	50.0 (1)	0 (0)	42.9 (3)	14.3 (1)	40.0 (2)	41.7 (6)	32.4 (6)	37.7 (12)
CPC	B	45.5 (5)	60.0 (6)	30.0 (3)	ND	0 (0)	0 (0)	25.0 (1)	45.2 (14)	8.3 (1)	26.8 (15)
	DNH	0 (0)	0 (0)	60.0 (6)	ND	0 (0)	0 (0)	25.0 (1)	20.0 (6)	8.3 (1)	14.2 (7)
	M	54.5 (6)	40.0 (4)	10.0 (1)	ND	100 (3)	0 (0)	50.0 (2)	34.8 (11)	50.0 (5)	42.4 (16)
DSB	B	50.0 (3)	31.6 (6)	33.3 (2)	57.7 (4)	25.0 (4)	ND	ND	43.2 (15)	25.0 (4)	39.5 (19)
	DNH	0 (0)	0 (0)	50.0 (3)	0 (0)	0 (0)	ND	ND	12.5 (3)	0 (0)	10.0 (3)
	M	50.0 (3)	68.4 (13)	16.7 (1)	42.9 (3)	75.0 (12)	ND	ND	44.5 (20)	75.0 (12)	50.6 (32)
OR	B	14.3 (1)	50.0 (11)	100 (4)	ND	100 (1)	66.7 (2)	14.3 (1)	54.8 (16)	60.3 (4)	57.6 (20)
	DNH	42.9 (3)	27.3 (6)	0 (0)	ND	0 (0)	0 (0)	42.9 (3)	23.4 (9)	14.3 (3)	18.9 (12)
	M	42.9 (3)	22.7 (5)	0 (0)	ND	0 (0)	33.3 (1)	42.9 (3)	21.9 (8)	25.4 (4)	23.6 (12)
Total	B	54.1 (33)	49.5 (47)	45.1 (23)	62.5 (5)	18.5 (5)	58.3 (7)	21.4 (6)	52.8 (108)	32.7 (18)	44.2 (126)
	DNH	6.6 (4)	8.4 (8)	43.1 (22)	0 (0)	14.8 (4)	25.0 (3)	50.0 (14)	14.5 (34)	29.9 (21)	21.1 (55)
	M	39.3 (24)	42.1 (40)	11.8 (6)	37.5 (3)	66.7 (18)	16.7 (2)	29.0 (8)	32.7 (73)	37.5 (28)	34.7 (101)

CBE and DSB, respectively, in 1996–1997, which also may have been raven predations. No evidence of predation on storm-petrels by peregrine falcons was found, although falcons were observed perched on cliffs, and flying near all sea caves on several occasions.

In 2005, evidence of predation of storm-petrels by island spotted skunks was detected at BC. On June 2, 60 storm-petrel carcasses, no active storm-petrel nests, and faint skunk odor were found. NPS personnel live-trapped and removed a single island spotted skunk from the cave on June 11. On July 28, 13 active storm-petrel nests were found, indicating

that temporary skunk-free conditions had allowed remaining adults to lay eggs. However, on September 15, no active nests and 16 more dead adult storm-petrels were present, following further predation by at least one other skunk. No further effort was made to remove skunks in 2005. In March 2006, NPS personnel set live traps at BC to test for the presence of skunks and none were detected. Nineteen and 28 active storm-petrel nests were observed in BC in 2006 and 2007, respectively, indicating no continuing skunk predation (Table 1).

DISCUSSION

Organochlorine Contaminants and Broken Eggshells

Between 1995–1998 and 2005–2007, hatching and breeding success at SCI apparently increased, although mainly at CPC, BC, and OR. Lower egg breakage in 2005–2007 than in 1995–1998 likely resulted to a great extent from decreased levels of organochlorine contaminants in ashy storm-petrels by 2008 compared to levels observed in 1992–1997 (Fry 1994; Kiff 1994; Carter et al. 2008b, unpublished data). In 1995–1998, 53% of unsuccessful eggs at SCI were found broken, in marked contrast to SEFI where only 4%–9% were broken in the 1965–1983 period (James-Veitch 1970; Ainley et al. 1990). These SEFI studies did not determine causes for broken eggs or eggs that were whole but did not hatch, although eggshell thinning was demonstrated in ashy storm-petrel eggs at SEFI in 1969–1970 (Coulter and Risebrough 1973). Approximately 30% of broken eggs found in nests at SCI in 1995–2007 were whole eggs with visible breaks, cracks, and dents; the other 70% were eggshell fragments only. Even with reduced contaminants, a slightly higher level of egg breakage may still occur at SCI than at SEFI. Egg neglect is well known in storm-petrels but was not quantified at SCI, due to the infrequency of our visitations. Some neglected or abandoned eggs at SCI may have been: a) cracked or broken by other storm-petrels in relatively dense sea cave and offshore rock colonies with several open nest sites; or b) in some locations (i.e., BC and CPC), eaten by small numbers of deer mice. Comparisons of natural levels of egg breakage at SCI and SEFI are confused by different study methods (which may lead to different percentages of broken, missing, abandoned, and unknown fate eggs), and different rates and causes of egg neglect and egg abandonment may exist between colonies and time periods of study. Only introduced house mice occur at SEFI but have not been documented to eat ashy storm-petrel eggs (Ainley et al. 1990). Few apparently viable eggs (i.e., whole non-cracked eggs) were not incubated by adults during our nest visits which might have been available for predation by small numbers of deer mice. Most broken eggs at SCI appeared to result from eggshell thinning.

Levels of chlorinated hydrocarbons are generally high in storm-petrels for reasons that are unclear (Boersma and Groom 1993). Eggshell thinning and egg breakage have been related to elevated levels of chlorinated hydrocarbons (Hickey and Anderson 1968; Anderson et al. 1969; Blus 1982). Based on ashy storm-petrel eggs collected at SCI in 1992, Kiff (1994) reported significant eggshell thinning (8.3%), in comparison to eggshells collected before 1947 (i.e., pre-DDT era), with 27.8% of eggs exhibiting > 15% thinning. Fry (1994) further reported relatively high levels (11.36 ppm) of DDT residues in these eggs. Based on eggs sampled in 1992, 1996–1997, and 2008, Carter et al. (2008b) reported significant declines in levels of both p,p-DDE (-8.8% per annum) and Total PCBs (-8.4% per annum) from 1992 to 2008. In 1992–1997, relatively high contaminant levels, and associated eggshell thinning and premature embryo deaths, likely contributed to relatively low hatching success and relatively high levels of broken eggs at SCI during this period and likely for decades beforehand. By 2008, contaminant levels were much lower, likely with much less remaining effect on reproductive performance. However, even with lower contaminant levels, broken eggs continued to occur in 2005–2007, likely reflecting continuing contaminant effects on certain individuals plus other factors causing continuing egg breakage.

Predation by Barn Owls

At SCI, the barn owl was the primary avian predator of storm-petrels, based on feather remains and contents of collected pellets (McIver 2002). Numbers of owl-killed storm-petrel carcasses recovered increased from 1995 to 1997, with 90% at BC, the location with the largest numbers of nests

(Table 1). Evidence of owl predation at OR remained low in 1995–1997, with two kills per year (McIver 2002). Avian predation at SCI was much reduced during 2005–2007, coincident with higher breeding success. James-Veitch (1970) observed ashy storm-petrels circling, hovering or fluttering over crevices as they returned to nesting areas. In addition, storm-petrels were seen at entrances of nest sites at dusk, apparently waiting to leave. Storm-petrel chicks older than 20 days also will leave nest sites and walk and flap their wings on the surface of the ground at night before returning to nest sites (James-Veitch 1970; Scott 1970; Mínguez 1997). These behaviors of adults and older chicks likely increase their detection by barn owls, which have excellent low-light vision (Dice 1945; Marti 1992) and hearing (Konishi 1973), and can discriminate sounds of appropriate prey by memorizing prey noises (Konishi and Kenuk 1975). At SEFI, western gulls and burrowing owls are significant predators of ashy storm-petrels, and may be largely responsible for a 30%–40% decline in population size of ashy storm-petrels between 1972 and 1992 (Sydeman et al. 1998a, 1998b).

Predation by Skunks

Large-scale predation of adults by island spotted skunks at BC in 2005 at first seemed to be an unusual event, with skunks apparently falling or jumping off nearby bluffs or cliffs and swimming into the otherwise inaccessible cave (McIver and Carter 2006). However, in 2008, skunks also entered CPC and killed at least 30 adults (McIver et al. 2009). Like other sea caves in which ashy storm-petrels nest at SCI, BC occurs at the base of sheer cliffs, which do not afford regular access to small mammals, except for small numbers of deer mice in certain caves (McIver 2002). Skunk populations on SCI have increased in recent years (Jones et al. 2008), which may somehow relate to greater potential for skunks to enter sea caves than in the recent past. The lack of skunk presence in sea caves from 1995 to 2004 was likely preceded by decades of skunk-free conditions to account for the large numbers of nesting storm-petrels first found in these sea caves in 1994 (Carter et al. 2007). Prior to 2005, BC had the largest number of nests of ashy storm-petrels at SCI (McIver 2002; Carter et al. 2007). By 2007, numbers of storm-petrel nests at BC were about 40% of pre-2005 levels, reflecting apparent return of some adults and past progeny that escaped skunk predation.

Night Lights

At OR, the number of active storm-petrel nests was 60% and 75% lower in 1997 than in 1995 and 1996, respectively (Table 1). Beginning in 1992, intense market squid harvesting using bright night lights occurred near SCI, and squid fishing activity was relatively high along the north coast from the west end to OR during October 1995, 1996, and 1997 (Maxwell et al. 2004). No direct observations or evidence of mortality of ashy storm-petrels through attraction to squid fishery lights were noted. However, ashy storm-petrels and related species are attracted to bright night lights, putting them at risk of light-related mortality or nest abandonment at or near breeding colonies (James-Veitch 1970; Reed et al. 1985; Ainley et al. 1990; Ainley 1995; Carter et al. 2000; Le Corre et al. 2002). Ashy storm-petrels likely first breed at 4–5 years of age as found for Leach's storm-petrels (Morse and Buchheister 1977; Huntington et al. 1996). Reduced breeding success and some adult mortality due to night lights at OR is consistent with population reduction in 1995–1997 (Carter et al. 2008a). A similar reduction in numbers of nests was not found at CBE and DSB in 1995–1998, apparently due to nesting in deep caves with few or no nesting gulls or owls nearby. Reasons for increases in numbers of ashy storm-petrel nests at OR in 2006–2007 are not fully understood and may reflect reduced night lights, movements of some adults from BC after skunk predation in 2005, or other factors.

Park Visitor Disturbance

Between 1995 and 2007, breeding success was lowest at CPC, which was easy to access by kayak and located approximately 0.75 km from Scorpion Anchorage, a popular SCI destination for camping and sea kayaking on NPS lands. In contrast, breeding success was greatest at DSB, which is difficult to access by kayak and located on Nature Conservancy lands at least 20 km from Prisoner's Harbor, the nearest SCI area on NPS lands with relatively high park visitor use. Human disturbance to seabird colonies during the breeding season can cause lowered breeding success, breeding failure, colony abandonment, destruction of nesting habitat, and deaths of adults, chicks, and eggs (Carney and

Sydeman 1999; also see Nisbet 2000). A few instances of non-researcher human visitation to CPC and BC were documented in 1995–2007 but our infrequent visits (often on weekdays) prevented measurement of non-researcher visitation rate. Incubating ashy storm-petrels are vulnerable to disruption of nesting activities by human visitations, especially at nests in open habitats at SCI sea caves. No specific instances of egg breakage or nest failure from non-researcher visitations were noted. However, peak numbers of kayakers occur during the incubation and early-chick periods in June–September. Non-researcher human visitation to CPC, which is the most accessible location closest to high visitor use areas, may have contributed to lower breeding success in 1995–2007.

Oceanographic Conditions and Breeding Success

As also found at SEFI (Ainley et al. 1990; Sydeman et al. 2001), reproductive performance of ashy storm-petrels at SCI showed limited inter-annual variability, with no clear correlation between warm-water years and reduced breeding success. In 1995–1998, breeding success at SCI was lowest in 1996, when weak to moderate La Niña (cool water) conditions prevailed (Schwing et al. 1997), and greatest in 1997 (65.2%), a year of transition from La Niña to El Niño (warm water) conditions (Lynn et al. 1998).

Competition for Nest Sites

Competition for nest sites can result in reduced breeding success in storm-petrels (Harris 1969; Ramos et al. 1997). At SEFI, ashy storm-petrels nested in shallower crevices than Leach's storm-petrels and did not excavate nesting burrows as Leach's did on occasion (Ainley et al. 1990). Leach's storm-petrels do not nest at SCI (Sowls et al. 1980; Carter et al. 1992), but some ashy storm-petrels likely compete for limited nest sites in dense-breeding conditions in sea caves with conspecifics along with small numbers of crevice-nesting pigeon guillemots, Xantus's murrelets (*Synthliboramphus hypoleucus*), and Cassin's auklets (*Ptychoramphus aleuticus*). Dense breeding in sea caves likely reflected unusual availability of many suitable nest sites in a relatively small area, limited suitable nesting habitat in adjacent steep cliffs, and strong attraction of conspecifics. Murrelets and auklets tend to nest earlier than ashy storm-petrels, and guillemots tend to use larger crevices than storm-petrels. Despite dense-nesting conditions, availability of suitable nest sites does not currently limit nesting storm-petrels at BC, CBE, and DSB but may be a factor at CPC and OR.

Management

Continued monitoring of ashy storm-petrels at SCI will be conducted to evaluate restoration efforts begun in 2008 that aim to reduce potential impacts of avian and mammalian predators, night lights, and human disturbance through the use of artificial nesting habitat, social attraction techniques, and greater protection of nesting areas (McIver et al. 2008, 2009). Long-term monitoring also is needed to determine how this globally rare species, petitioned for listing in 2007 under the U.S. Endangered Species Act, responds to various factors that influence reproductive performance. Future research, greater statistical analysis of existing data, and statistical comparisons to SEFI are needed to further explore certain factors affecting reproductive performance at SCI, especially pollutants, predation, and climate change.

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NEST SITE SELECTION OF THE ENDEMIC "DUSKY" ORANGE-CROWNED WARBLER (*VERMIVORA CELATA SORDIDA*) ON SANTA CATALINA ISLAND

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Abstract—The *sordida* subspecies of orange-crowned warbler (*Vermivora celata*) often nests off-ground, unlike mainland populations. Here, we quantitatively describe nest site selection during one breeding season in two contrasting habitats, xeric and mesic, to better understand adaptive nest site selection. As expected, the Catalina Island orange-crowned warbler exhibited a high level of plasticity in nest site location with larger variation in nest heights when compared with mainland subspecies. We found that only canopy cover above nests was statistically different between the xeric and mesic habitats, being lower in the xeric habitat. There was also a wider variety of substrates utilized in the mesic habitat, which was likely related to differences in substrate diversity. There was a significant preference for a northeast orientation of nests and nest entrances in the mesic habitat, but a preference for nest entrances to be orientated west on the xeric plot. Nest and nest entrance orientation were highly correlated with the aspect of the slope on which the nest was situated.

INTRODUCTION

Various selection pressures act on nest site choice and have led to the evolution of a diverse array of nest structures, ranging in size, shape, nest construction materials, attachment of the nest to the chosen substrate, and nest location (Hansell 2000). Birds living in a heterogeneous environment have a variety of choices for potential nest placement, but these options may be limited by types of predators present (Remeš, 2005), interspecific or intraspecific competition for these sites (Svärdson 1949; Liebezeit and George 2002), or purely logistical restrictions such as sufficient physical support for large nests built by species with large body size (Hansell 2000). For example, birds may choose certain nest sites to avoid predators (e.g., Clark and Shutler 1999; Martin et al. 2000; Holway 1991; Weidinger 2002) or to allow a greater ability to see approaching predators (e.g., Götmark et al. 1995). Sites may also be chosen to provide a favorable microclimate for offspring development (see review by Webb 1987). Consequently, nest site selection is often highly conserved in most species, such that populations occupying different environments will select similar nest sites (Baicich and Harrison 1997). For example, birds may choose a very specific orientation for the nest (e.g., Finch 1983; Hoekman et al. 2002; Burton 2006) or nest entrance (Facemire et al. 1990).

An example of a group that exhibits a stereotypical nest site choice is the genus Vermivora. In North America, the majority of these warblers nest on or close to the ground (Baicich and Harrison 1997). An exception to this pattern is found on Santa Catalina Island, California, where the endemic "dusky" orange-crowned warbler (*Vermivora celata sordida*) breeds and nests in a wide range of sites (H. Montag, personal observation). The dusky orange-crowned warbler is endemic to the California Channel Islands, which represent the southern edge of the species' breeding range. Dusky orange-crowned warblers have a mean body mass of 9.4 g (S.E. = 0.8g; n = 106) with

the males of this subspecies being significantly larger than the females (5%–6%; n = 106; Sogge et al. 1994). Both initial and replacement nests are initiated between February and June (H. Montag, personal observation). The female lays two to four eggs, two to three days after nest completion, and incubation starts on the day that the last (Sogge et al. 1994) or penultimate egg (H. Montag, personal observation) is laid. Only the female incubates, usually for 12 days, and all eggs hatch within 24 hr of each other. Nestling period is 11–13 days (Sogge et al. 1994).

On Santa Catalina Island, *V. celata sordida* inhabits a wide variety of ecosystem types, and populations of this species are especially dense, with around five breeding pairs per ha (H. Montag, personal observation). The endemic subspecies experiences very little interspecific competition for nesting locations, due to the fact that there are few other nesting passerines which utilize the same nesting substrates (mainly Hutton's vireo, *Vireo huttoni unitti*; spotted towhee, *Pipilo maculatus clementae*; chipping sparrow, *Spizella passerina arizonae*; and Pacific slope flycatcher, *Empidonax difficilis*) and so is not competitively excluded from specific nesting sites, as has been shown in other studies (Svärdson 1949). This provides us with an opportunity to study nest site choice in a situation where a wide variety of nest sites are available and choice is not limited by competition. In this study, we measured characteristics of dusky orange-crowned warbler nests and nest sites over one breeding season in a mesic and a xeric habitat. Our aim was to quantitatively describe the nesting site of the endemic orange-crowned warbler population on Santa Catalina Island, and to explore whether warblers would take advantage of the wide variety of nest sites available, or whether choice of nest site characteristics would be constrained due to selection pressures other than competition.

MATERIALS AND METHODS

Study Plots and Species

The study was undertaken on Santa Catalina Island, Los Angeles County, California, USA (33°22'30"N, 118°25'56"W) from March to May 2006. The study area was in Bulrush Canyon, a large east-west oriented valley located near the southwest coast of the island. The fieldwork was conducted on two plots, one mesic in the structure of its habitat and one xeric. The mesic plot was situated in the bottom of Bulrush Canyon, on a north-facing slope, where the habitat consists of creek beds (often dry), scrub oak (*Quercus pacifica*) and toyon (*Heteromeles arbutifolia*) dominated woodland, lemonade-berry (*Rhus integrifolia*), and large "meadow" areas composed of grasses and forbs. Average elevation for nest sites on this plot was 73.95 ± 3.1 m above sea level (n = 42). In comparison, the xeric plot included a south-facing slope and a ridge top. The vegetation was less diverse and was dominated by coastal sage (*Artemesia californica*) and prickly pear cactus (*Opuntia* ssp.). The average elevation for nest sites on this plot was 86.13 m (S.E. = 3.4 m; n = 14). Each study plot covered 500 x 300 m, and was gridded with flagging every 25 m and assigned a letter/number to facilitate mapping of territories and nests.

Nest Measurements

We searched for nests from 6 a.m. to 1–3 p.m. each day following methods in Martin and Geupel (1993). Bird behavior and vocalizations were closely observed and plots were methodically searched. A total of 56 orange-crowned warbler nests were found, 42 on the mesic plot and 14 on the xeric plot. Subsequent to failing or fledging, we collected detailed quantitative descriptions of nests and nest sites. This was done from day 25 to 30 (after clutch completion) to standardize the timing of measurements for each nest, as nest site characteristics can change over time (Burhams and Thompson 1998). We took the following measurements using a variation of the BBird protocol (Martin et. al. 1997): nest height, substrate, number and diameter of support branches, nest and nest entrance orientation, aspect, concealment, canopy cover, nest dimensions, and volume.

Nest height was measured from the base of the exterior of the nest to the ground below. For six nests that were inaccessible, nest height was visually estimated. Nests with height = 0 cm were categorized as "ground" nests, while nests with height > 0 cm were categorized as "off-ground" nests. For all off-ground nests, we recorded the species of plant(s) that the nest was placed in. Grass, twigs, and lichen were not identified to species. In addition, we recorded the status of the substrate

(alive or dead), the number of branches supporting the nest that were accessible or intact, and the diameter of the largest support branch. Substrate availability data were not collected for either site.

Orientation for nests and nest entrances were only measured for off-ground nests (n = 42). Nest orientation was assessed by directing a compass from the center of the nest substrate towards the nest and recording the bearing. The nest entrance was determined to be the most direct gap in the vegetation to the nest, also taking into account any flattened surface on the rim (indicating where adults perch in order to feed nestlings) and personal observations of the adults' flight patterns. For 34 nests with a measurable entrance, orientation of the entrance was measured in a manner similar to orientation of the nest. We also measured the orientation of both nest and nest entrance relative to downhill in order to explore any preference, as has been found in other studies (e.g., Roseberry and Klimstra 1970), that may aid in adult predator avoidance through ease of escape from the nest. Aspect for the 42 off-ground nests was measured by standing at the nest site, directing a compass downhill from that point and taking a bearing. Seven of these readings were omitted from the analysis due to a recording error. The angle between the orientation of the nest or nest entrance and the aspect of the slope was then calculated (i.e., 0º would be directly downhill, 90º would be at a right angle from downslope, and 180º would be upslope).

Concealment was measured as the percentage of the nest that was covered by vegetation. Mean lateral concealment was calculated by visually estimating concealment from 1 m away from the nest in each cardinal direction, then taking the average of these four measurements. Concealment was also assessed from above and from below (for elevated nests). Canopy cover was assessed by using a 35mm Fisheye Camera with 170º lens (Lomography, New York) to take a picture of the vegetation above the nest sites. The film was developed and converted into an electronic format using a negative scanner. Canopy cover was then calculated using Gap Light Analyzer software (Version 2.0, Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY).

The dimensions of the nest were calculated as follows: outer height (from rim of the nest to base of the exterior), nest cup depth (from rim of the nest to base of inner cup), outer diameter (the diameter of the widest exterior part of the nest) and inner diameter (the diameter of the inner cup). Volume was calculated assuming a regular ellipsoid with equal width and depth, using the following equation (adapted from Lombardo 1994):

$$\text{Nest volume} = \frac{4/3\pi(w/2)h(d/2)}{2}$$

where both w (width) and d (depth) are equal to outer nest diameter, and h (height) is outer nest height.

SPSS 14.0 software (SPSS Inc, Chicago, IL) was used to analyze data. We used chi-square contingency tests to compare frequencies of substrate types and dead vegetation used for nests between the mesic and xeric plots. A chi-square contingency test was also used to compare the frequencies with which nests were observed off the ground between the two habitats.

Because the orientation data are considered to be circular data, we used Oriana 2.0 (Kovach Computing Services, Anglesey, Wales) to obtain circular graphs and mean vectors for nest and nest entrance orientation. Rao's spacing U-test was run on orientation data to compare distributions of orientations between mesic and xeric plots and to assess non-random preference for orienting nests or nest entrances in a particular direction. Rao's spacing test has been shown to be the most powerful statistical test for circular data and it is especially useful for polymodal distributions and with small sample sizes (Bergin 1991). Oriana does not give exact P values for this test, so we only report these values incrementally (e.g., P>.05, P>.1). Nests located in the center of the substrate were omitted from analyses of nest orientation on the substrate, as they had no particular bearing. We used a Watson-Williams F test to compare the orientation of nest entrances between mesic and xeric plots, as Oriana utilizes this test to compare two or more samples to explore if their mean angles differ significantly.

To test whether there was a bias to orient nests or nest entrances downhill, we used chi-square tests to compare the frequencies of nests/nest entrances oriented downhill versus upslope. A t-test was used to compare the mean angle between nest orientation and downhill between the two habitats, and a circular-circular correlation was used to examine

the relationship between nest site aspect and nest entrance orientation.

Two factor analysis of covariance was used to test the effects of habitat type (mesic/xeric) and nest height (on-/off-ground) on mean nest height, number of support branches, diameter of largest support branch, concealment, canopy cover, nest volume, and nest cup depth. For response variables that were only measured for off-ground nests, we used single factor analysis of covariance to compare means between xeric and mesic habitats. Means are reported with ±1 standard deviation.

RESULTS

We located orange-crowned warbler nests in 12 different vegetation substrates, with lemonade-berry being the most common overall (Table 1). The types of substrates used differed significantly between the two plots (χ^2=10.72, df=4, P=0.03), with lemonade-berry, grass and trees being utilized more commonly on the mesic plot, and sagebrush being used predominantly on the xeric plot. However, we did not measure availability of these plants on each plot, and so conclusions in terms of preference are not quantifiable. Use of dead plant material was common, with 46% (n = 35) of nests placed in dead vegetation (Table 1). Between the mesic and xeric plots, there was no significant difference in the use of dead vegetation as the nesting substrate (χ^2=0.4, df=1, P=0.53) or in the number or width of branches supporting the nest (Table 2). Although canopy cover was higher for nests on the mesic plot than on the xeric plot (Table 2), there was no significant difference in nest concealment from above, below, or laterally (Table 2). Ground nests showed both higher lateral concealment and concealment from above than elevated nests (Table 2).

Means and standard deviations of nest height and nest characteristics are presented in Table 2. Of

Table 1. Numbers of orange-crowned warbler nests found in different substrates in two study plots on Santa Catalina Island, California. Nests that were placed in more than one substrate species are recorded in multiple substrate categories.

Substrate	Status	Mesic	Xeric
Lemonade-berry (*Rhus integrifolia*)	Live	15	4
	Dead	3	2
Coastal sagebrush (*Artemesia californica*)	Live	2	4
	Dead	2	3
Harding grass (*Phalaris aquatica*)	Live	3	–
	Dead	4	–
Narrow leaved bedstraw (*Galium angustifolium*)	Live	–	1
	Dead	–	1
California ivy (*Hedera helix*)	Live	1	–
	Dead	1	–
Honeysuckle (*Lonicera spp*)	Live	–	–
	Dead	2	–
Oak (*Quercus pacifica*)	Live	1	–
	Dead	6	–
Willow (*Salix spp*)	Live	1	–
	Dead	1	–
Toyon (*Heteromeles arbutifolia*)	Live	2	1
	Dead	–	–
Grass	Live	–	–
	Dead	1	–
Twigs	Live	–	–
	Dead	1	–
Lichen	Live	1	–
	Dead	–	–

Table 2. Means and standard deviations of nest site characteristics for on- and off-ground nests of dusky orange-crowned warblers on two study plots on Santa Catalina Island, California. Also presented are results of ANCOVA tests comparing nest site characteristics between ground and off-ground nests and between mesic and xeric habitats.

					ANCOVA Test	
Nest-site characteristic	On-ground nest average	Off-ground nest average	Mesic plot average	Xeric plot average	On-/off-ground nests	Mesic/xeric
Nest height (cm)	N/A	1±0.8 *n* = 41	1.1±1 *n* = 32	0.7±0.4 *n* = 9	–	$F_{1,54}$=1.14 P=0.29
Nest volume (cm³)	374±305 N = 13	706±380 *n* = 35	676±359 *n* = 35	609±239 *n* = 13	$F_{1,46}$=5.8 P=0.02	$F_{1,45}$=0.48 P=0.49
Nest cup depth (cm)	3.7±0.4 N = 13	3.9±0.5 *n* = 35	3.8±0.8 *n* = 35	4±0.1 *n* = 13	$F_{1,46}$=1.07 P=0.31	$F_{1,45}$=0.91 P=0.35
No. support branches	N/A	13.5±11.9 *n* = 29	15±14 *n* = 21	9.5±4.6 *n* = 8	–	$F_{1,27}$=1.27 P=0.27
Diameter of largest support branch (cm)	N/A	1.2±1.7 *n* = 29	1.3±1.7 *n* = 21	1.1±1.6 *n* = 8	–	$F_{1,27}$=0.12 P=0.73
Mean lateral concealment (%)	98±4 *n* = 13	79±20 *n* = 29	78±5 *n* = 30	84±5 *n* = 12	$F_{1,40}$=12.3 P=0.001	$F_{1,39}$=0.11 P=0.74
Concealment from above (%)	90±14 *n* = 13	66±26 *n* = 29	67±5 *n* = 30	59±13 *n* = 12	$F_{1,40}$=9.77 P=0.003	$F_{1,39}$=0.07 P=0.79
Concealment from below (%)	N/A	65±31 N = 29	72±7 *n* = 21	51±10 *n* = 8	–	$F_{1,27}$=1.68 P=0.21
Canopy cover (%)	86±11 N = 10	86±14 N = 32	90±2 *n* = 31	74±8 *n* = 11	$F_{1,39}$=0.05 P=0.82	$F_{1,40}$=7.27 P=0.01

the 56 nests found, a significantly larger number of nests were elevated (73%) than were placed on the ground (χ^2=12.07, df=1, P=0.001). There was no significant difference in the proportion of nests placed on- and off-ground between the mesic and xeric plots (χ^2=0.76, df=1, P=0.38). Nest cup depth was not significantly different between ground and off-ground nests or between habitats (Table 2). There was also no significant difference in nest volume between habitats. However, nests elevated off the ground were significantly larger in volume than those on the ground (Table 2).

For both plots combined, 22 of the 42 off-ground nests (55%) were placed in the center of the substrate. Of the remaining 19 nests, the mean vector of nest orientation was 41 ± 77º (NE; *n* = 19), with no significant difference in orientation between the two study plots (Rao's spacing test, U=33, P>0.5 *n* = 19). Nest entrance orientation was significantly different between the mesic and xeric plots (Watson-Williams F=5.74, P=0.023, *n* = 34), with mean nest entrance orientation vectors of 40 ± 103º (NE; *n* = 24) on the mesic plot, and 281 ± 104º (W; *n* = 10) for the xeric plot. For the mesic plot, Rao's spacing test indicated a significant preference in orienting nest entrances to the northeast (U=165, P<0.05, *n* = 24; Fig. 1). For the xeric plot, Rao's spacing test indicated a significant preference to orient nest entrances to the west (U=172, P<0.05, *n* = 10; Fig. 1).

When looking at both plots combined, the mean angle of the nest orientation in the substrate from downhill was 41 ± 42º (*n* = 15, range 0–140º) and mean orientation of nest entrance from downhill was 71.9 ± 53º (*n* = 29, range 10–180º). Since both of these figures are less than 90º, they suggest a preference to orient nests and nest entrances downhill. The chi-square tests found this preference

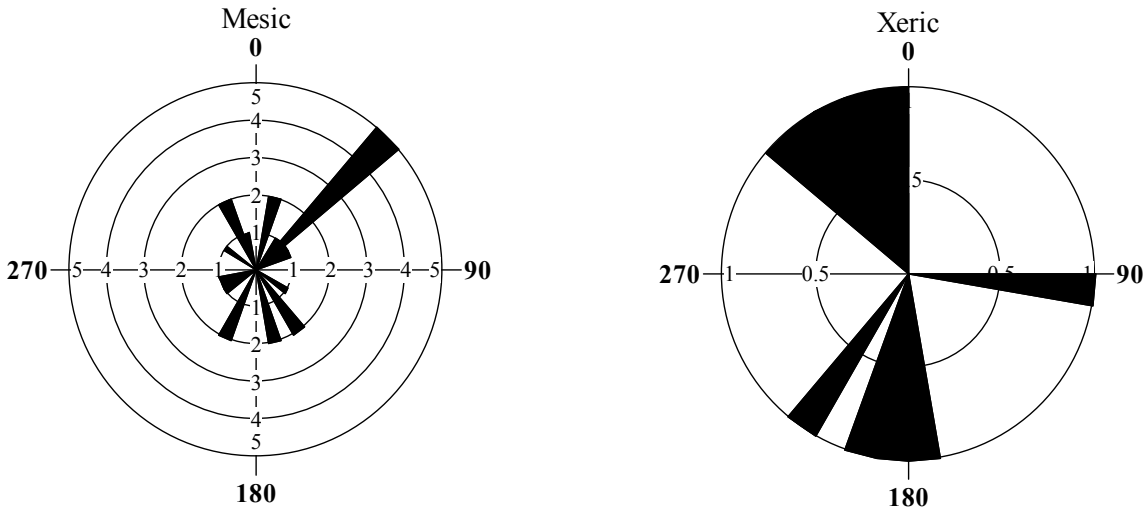

Figure 1. Circular histograms showing orientation of nest entrance for orange-crowned warblers in mesic and xeric habitats on Santa Catalina Island, California. Numbers inside the circles represent numbers of nests. Numbers on the outside represent compass bearing, with 0° indicating nest entrances oriented to the north.

significant for both nests (χ^2=8.1, df=1, P=0.01; Fig. 2) and nest entrances (χ^2=4.17, df=1, P=0.04; Fig. 2). Orientation of nests on substrate relative to downhill did not differ significantly between xeric and mesic plots (t=1.06, df=26, P=0.3). The mean aspect of all nests was 11.9 ± 83.3º (N; *n* = 35), likely attributable to most of the nests being observed on the mesic plot, which was situated on a north-facing slope. Aspect of the nest site and direction of nest entrance were significantly positively correlated (with a circular-circular correlation *r* = 0.15, *n* = 29, P<0.05).

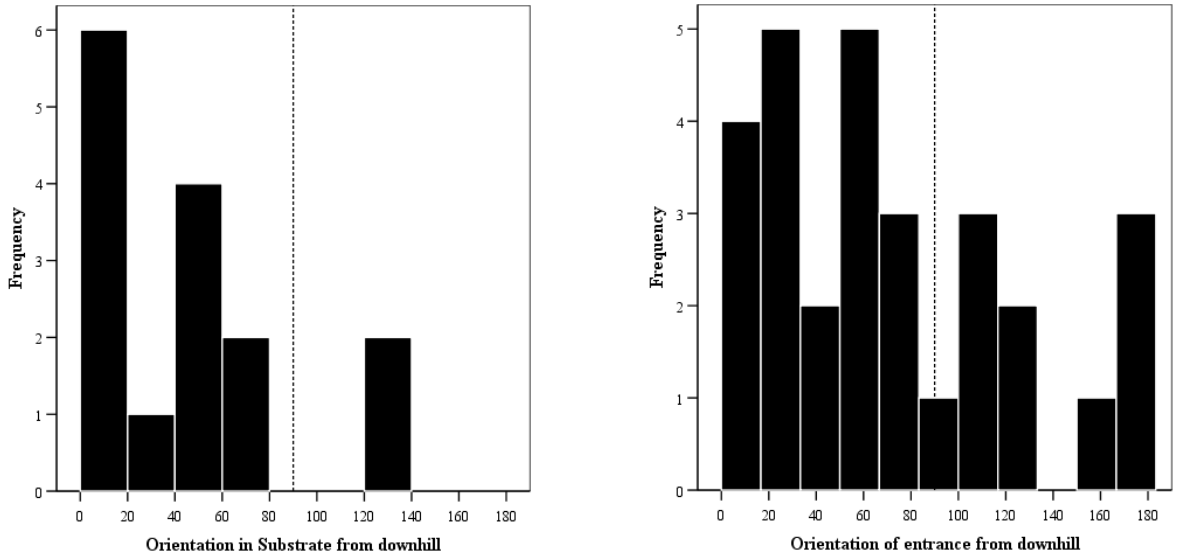

Figure 2. Orientation of both nests (left figure) and nest entrances (right figure) relative to downhill for orange-crowned warblers on Santa Catalina Island, California. Dotted lines represent flat ground at 90º; nests and nest entrances to the left of this line are oriented downhill.

DISCUSSION AND CONCLUSIONS

Dusky orange-crowned warblers on Santa Catalina Island utilize an array of nesting sites. Warblers appeared to utilize the nesting substrates most commonly found on their respective habitats, with coastal sage being most commonly used on the xeric plot and lemonade-berry being predominantly used on the mesic plot. Although no quantitative analysis of vegetation abundance was performed, personal observations by H. Montag were that the most widespread shrub on the xeric plot was coastal sage brush, whereas lemonade-berry was more common on the mesic plot. Thus, nest site selection may be purely due to availability, or it may be related to the 'potential nest site' hypothesis (Martin and Roper 1988), where birds may place nests at a site where there are many other similar sites nearby, to reduce predator search efficiency. Further study of the vegetation surrounding the nest site is needed to explore this. The greater array of nesting substrates on the mesic plot is probably due to the increased availability of different plants on this site (H. Montag, personal observation), although again, this needs to be quantitatively assessed. Off-ground nests tended to be larger, which may be explained by structural necessity, as off-ground nests may need more supportive material (such as twigs). This would need further investigation into nesting materials utilized. Although canopy cover on the xeric plot was lower, possibly due to the vegetation on this plot being comprised primarily of shrub-like species, nest concealment from any direction was not different from the mesic plot. The widespread utilization of dead vegetation as a nesting substrate may increase the crypsis of the nest as orange-crowned warbler nests are composed of predominantly dead plant material.

We observed most nests to be elevated off the ground, despite elevated nests being less concealed than ground nests. These results differ greatly from accounts of other orange-crowned warbler subspecies, which place their nests on or close to the ground (Sogge et al. 1994; Baicich and Harrison 1997). There has been only one study which describes off-ground nests in a mainland population (Zyskowski 1993), in which only of 3 of 131 (2.3%) nests found were above ground, ranging in height from 2 to 3.2 m. On Santa Catalina Island, 73% of nests were placed off-ground and the average height for elevated nests was 1 m. The larger variation in nest heights on Catalina compared to mainland populations may be due to the process of ecological release; there are only seven other cup-nesting passerines on Catalina and therefore little competition for nest sites. Alternatively, nest predation alone, or in combination with ecological release, may explain the diversity of nest sites. Several snake and mammal species, but no bird species, are suspected of depredating warbler nests: gopher snake (*Pituophis melanoleucus*), Santa Catalina Island fox (*Urocyon littoralis catalinae*), Santa Catalina Island deermouse (*Peromyscus maniculatus catalinae*), and Beechey's ground squirrel (*Spermophilus beecheyi nesioticus*). Both feral cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) are present on the island and probably depredate warbler nests as well. These potential nest predators preferentially depredate ground nests, and the probability of nest predation declines with increasing nest height on Catalina (Peluc et al. 2008). Interestingly, there are no jays on Catalina, which are thought to prey on predominantly off-ground nests, but warblers still respond to the perceived presence of jays by shifting their nest sites to the ground (Peluc et al. 2008).

Most nests were placed centrally in the substrate, which may impede predators by maximizing vegetation obstruction. Of the remaining nests, there was a significant preference for nests to be orientated to the northeast, or downhill in relation to the nest site aspect. Nest entrances were orientated northeast on the mesic plot, but west on the xeric and these too corresponded with the aspect of the slope, although this may be due to differences in the general aspects of the plots. Preference for nest entrance has been found in other studies (Austin 1974; Facemire et al. 1990), as well as actual nest orientation (Hartman and Oring 2003; Burton 2006). Reasons for this preference may be due to microclimatic factors or that most nests were found on a north-facing slope. This can be seen in the relationship between nest orientation and nest entrance orientation in relation to aspect; dusky orange-crowned warblers place nests in the section of the substrate which corresponds with the downhill direction of the slope. An explanation for this may be in terms of an escape strategy for the adult birds. It was noted that when flushing birds from the nest (either to target

net nests or nest check) the adults always flew downslope. It is assumed that this is due to the easiest and fastest route from the nest in order to avoid adult predation.

This study provides the first detailed description of the nest site location of a subspecies which is very poorly understood. Further analysis of nest locations and predation will be carried out to assess the relationship between choice of nest site and its impact on reproductive success. Future research may compare these characteristics to the nests and nest sites of other orange-crowned warbler subspecies, which are found in a vast array of different habitats, including coniferous, riparian, mixed woodland, burn areas, etc. and in elevations ranging from sea level to 2350 m (Sogge et al. 1994).

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REPRODUCTIVE CONSEQUENCES OF AN EXTREME DROUGHT FOR ORANGE-CROWNED WARBLERS ON SANTA CATALINA AND SANTA CRUZ ISLANDS

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Abstract—Bird populations on the California Channel Islands are adapted to a Mediterranean-type climate with extended dry periods and considerable annual variation in rainfall. The winter of 2006–2007, however, was outside the normal range in southern California and ranked as one of the driest on record. Here we report how these drought conditions affected the reproductive output of a small songbird, the "dusky" orange-crowned warbler (*Vermivora celata sordida*), on Santa Catalina and Santa Cruz islands in the spring of 2007. Warblers on Catalina Island began establishing territories in February, yet they did not commence breeding activities until mid-April. Even then, only 5 of 45 females built nests and only 1 female laid eggs. The young in that nest ultimately starved; thus, the reproductive output of our study population on Catalina Island was zero. This contrasts starkly with the population on Santa Cruz Island, where all individuals studied attempted to reproduce and began nesting in mid-March. Nevertheless, only 11% of Santa Cruz Island warbler pairs fledged young due to high nest predation. Taken together, our observations from the two islands reveal marked differences in the consequences of severe drought and in the factors that limit the reproductive output of terrestrial birds on the Channel Islands.

INTRODUCTION

Climatic extremes can have a profound effect on community processes. The productivity of plants, the demography of animals, and their phenology relative to one another are all influenced by local and regional weather patterns (Stenseth et al. 2002; van Asch and Visser 2007). In the case of birds, variation in climate has been linked to variation in the timing of reproduction (Wilson and Arcese 2003; Visser et al. 2006), breeding productivity (Boag and Grant 1984; Gaston et al. 2006), and survival (Sillett et al. 2000; Mazerolle et al. 2005), with subsequent effects on population numbers (Boag and Grant 1981; Jones et al. 2003). Most of these responses to climate variability have been attributed to bottom-up processes, or the influence of organisms at lower trophic levels (e.g., insects) on the demography of organisms dependent on them for food (e.g., birds; Newton 1998). However, a range of other factors, including variability in phenological cues (e.g., temperature; Sherry et al. 2007) and top-down processes (i.e., predation; Ostfeld and Keesing 2000), can also drive demographic responses of wild populations.

In arid and semi-arid regions, water is a principal limiting factor and precipitation extremes can lead to drastic changes in primary productivity and community dynamics (Noy-Meir 1973). Organisms in these environments are adapted to withstand long periods of drought, and to respond opportunistically when precipitation gives rise to a greater availability of resources (Cody and Mooney 1978). Furthermore, because of the resource-limiting nature of these environments, secondary and tertiary consumers in arid regions tend to be primarily limited by bottom-up processes (Turner and Chew 1981), with demographic rates that are closely tied to variation in rainfall and food availability (e.g., Polis et al. 1997; Lima et al. 1999; Greenville and Dickman 2005). For example, widespread reproductive failure can be common in passerine birds when food is scarce during periods of drought (Boag and Grant 1984; Morrison and Bolger 2002), a phenomenon that appears to be

limited to birds breeding in arid and semi-arid regions (Bolger et al. 2005).

Here, we report how a severe drought affected orange-crowned warblers (*Vermivora celata sordida*) breeding on the California Channel Islands. The islands are located within a Mediterranean climate zone characterized by dry conditions during the breeding season and considerable annual variation in rainfall (Cody and Mooney 1978). The winter of 2006–2007, however, was outside the normal range and ranked as one of the driest on record (National Weather Service 2007). We monitored the breeding activities of orange-crowned warblers on Santa Catalina and Santa Cruz islands during the spring of 2007 and report substantial variation in the degree to which this severe drought affected warblers breeding on the two islands.

MATERIALS AND METHODS

We studied orange-crowned warblers on a 10 ha plot in Bulrush Canyon on Santa Catalina Island (33°20'N, 118°26'W; hereafter Catalina) and on an 18 ha plot in Coches Prietos Canyon on Santa Cruz Island (33°58'N, 119°42'W; hereafter Santa Cruz). The plots were delimited into 25–50 m grids with flagging tape to facilitate mapping of warbler territories and monitoring warbler breeding activity. Our work began on Catalina in 2003 and on Santa Cruz in 2005. Both plots were located within mesic drainages and were representative of high quality habitat for *V. c. sordida* on the islands, with vegetation that is dominated by island scrub oak (*Quercus pacifica*), lemonade berry (*Rhus integrifolia*), toyon (*Heteromeles arbutifolia*), and ceanothus (*Ceanothus* sp.).

We closely monitored breeding pairs within the study plots for the duration of the March-May breeding season, and in 2007 complete reproductive data were obtained for 45 pairs on Catalina and 18 pairs on Santa Cruz. Fewer territories were monitored on Santa Cruz because *V. c. sordida* are extremely cryptic there, perhaps due to the presence of the island scrub-jay (*Aphelocoma insularis*), a visually oriented nest predator (Curry and Delaney 2002). Most males (40 of 45 on Catalina, 16 of 18 on Santa Cruz) and some females (14 of 45 on Catalina, 4 of 18 on Santa Cruz) were marked with a unique combination of three colored plastic and one aluminum USFWS leg bands to enable individual identification. We visited territories every 1–3 days to 1) map territory boundaries, 2) locate nests, 3) determine laying dates, 4) count eggs and nestlings, and 5) monitor nest fates. Nestlings that survived to day seven after hatch were weighed, measured, and banded.

On both islands, we measured food abundance by sampling arthropods on branch clippings taken from island scrub oaks (methodology as per Johnson 2000). This technique is appropriate for orange-crowned warblers because they are foliage-gleaning insectivores (Sogge et al. 1994) and, in the case of populations on Catalina and Santa Cruz islands, focus their foraging efforts on oaks (Ghalambor and Sillett, unpublished data). Every two weeks, 12 points were randomly selected throughout each study plot and a 30 x 30 cm branch clipping was collected from the nearest oak. Samples were placed in individual plastic bags and frozen for at least 24 hr. After carefully inspecting and collecting arthropods from the frozen vegetation, leaves were removed from stems and weighed (to 0.1 g). The arthropods were stored frozen until they could be separated into adult insects, Lepidopteran larvae, and spiders, and then dried in an oven (at 80°C) and weighed on an electronic balance (to 0.0001 g). We calculated arthropod biomass for each branch clipping in milligrams of dry mass per gram of wet vegetation collected.

On Catalina, we surveyed oaks for new growth in April 2007 to determine the extent of leaf-out. Each week, we randomly selected 30–50 oaks throughout the study plot and examined each for leaf growth. The percentage of oaks with new leaves did not vary across the four weeks of the survey; therefore, we pooled data for statistical analysis. A GPS location was determined for each oak, and we used ArcGIS (ESRI 2007) to calculate the percentage of oaks that had grown new leaves within 40 m of the center of each warbler's territory. A buffer size of 40 m was chosen because 20 m, the average radius of an orange-crowned warbler territory on the Catalina study plot, yielded too small a sample size for most territories.

Rainfall data were obtained from weather stations located in Middle Ranch on Catalina (33°21'N, 118°26'W; Catalina Island Conservancy)

and in the Central Valley on Santa Cruz (33°60'N, 119°43'W; Western Regional Climate Center). Data were available from both weather stations for 13 years during the period 1990–2007, although data were not available for Santa Cruz in some years. Because the Channel Islands receive the vast majority of precipitation from November to April, we report winter rainfall and define it as that which fell from November in year *x*-1 to April in year *x*.

We used general linear models and program JMP IN (SAS Institute 2003) for all statistical analyses. Data were transformed when necessary to meet model assumptions. However, we report all summary data as untransformed means ± one standard error.

RESULTS

Climatic Conditions

Rainfall patterns on the Channel Islands are highly variable from year to year. Wet years on Santa Cruz tend to be wet years on Catalina (Fig. 1), although the former receives more precipitation over the course of most winters than the latter (Santa Cruz, 44.2 ± 6.9 cm, $n = 13$; Catalina, 36.0 ± 5.6 cm, $n = 13$; paired t-test, $t_{12} = 2.6$, $P = 0.02$). That was the case during the winter of 2006–2007, when Santa Cruz received 14.9 cm of rain from November to April and Catalina only received 9.1 cm, rainfall totals that were well below the long-term average for both islands.

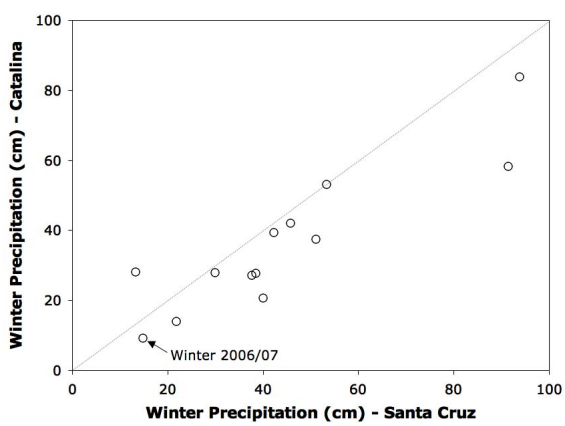

Figure 1. Winter precipitation (November to April) on Catalina and Santa Cruz islands for 13 years during the period 1990–2007 (data were not available for Santa Cruz in all years). Most of the points fall below the 1:1 line, indicating Catalina tended to receive less precipitation than Santa Cruz. Data are from the Catalina Island Conservancy (Catalina) and the Western Regional Climate Center (Santa Cruz).

Table 1. Number of orange-crowned warbler (*Vermivora celata sordida*) territories with nests, eggs, and fledged young on Santa Cruz and Santa Catalina islands during the 2007 breeding season, of the 18 and 45 territories that were monitored, respectively. Territories with unpaired males were not included. More females built nests and laid eggs on Santa Cruz than on Catalina (Fisher's Exact Test, P < 0.0001 for both), but there was no difference between islands in the proportion of territories that fledged young (Fisher's Exact Test, P = 0.08).

	Santa Cruz (n=18)	Catalina (n=45)
Nests	18 (100%)	5 (11%)
Eggs	17 (94%)	1 (2%)
Fledged young	2 (11%)	0 (0%)

Warbler Reproduction

The drought of 2006–2007 affected orange-crowned warblers breeding on Catalina more so than those on Santa Cruz. On both islands, most male *V. c. sordida* established breeding territories by late February and paired with females by mid-March. The initiation of nesting activities, however, occurred much later on Catalina than on Santa Cruz. The first nest was found on March 17 on Santa Cruz, and the first egg was laid eight days later. In contrast, we found the first nest on Catalina on April 10 and the first egg 12 days later, amounting to a difference of 24 and 28 days, respectively, for nest detection and egg laying between the two islands. The proportion of females that attempted to breed also differed between islands. On Santa Cruz, all of the females whose territories were monitored built nests and 94% were confirmed to have laid eggs, whereas on Catalina only 11% of the females built nests and even fewer (1 of 45) laid eggs (see Table 1). Despite this stark difference in breeding attempts, reproductive output was similarly poor on both islands. Because of high predation rates on Santa Cruz (daily nest mortality: 0.09 ± 0.02; Sofaer et al., unpublished manuscript), only two territories were successful in fledging young. On Catalina, the only nest where eggs were laid failed due to the nestlings starving. Mean nestling mass in this nest was 4.5 g on day seven, much less than for nestlings on Santa Cruz in 2007 (8.4 g, $n = 1$ nest) and on Catalina from 2003–2006 (8.2 ± 0.1 g, $n = 71$ nests).

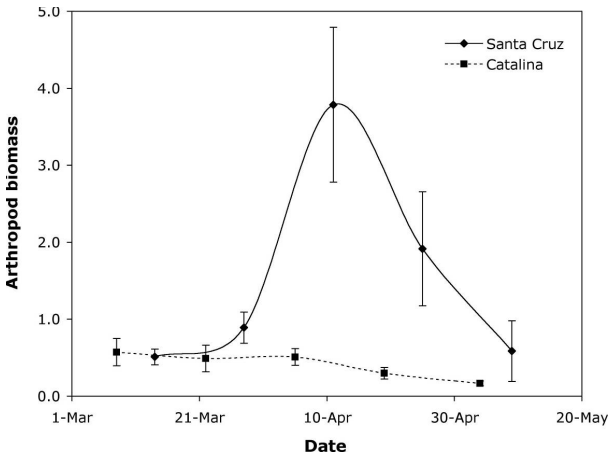

Figure 2. Arthropod biomass (in mg of dry mass per gram of wet vegetation; mean ± SE) during the 2007 breeding season, as measured through branch clippings collected from island scrub oak (*Quercus pacifica*) bi-weekly on both islands (n = 11 or 12 for each point).

In the end, the mean number of young fledged per warbler pair on Santa Cruz in 2007 was 0.4 ± 0.3 (n = 18); no young were fledged on Catalina (n = 45).

Food Abundance

Orange-crowned warblers on Santa Cruz had more food available in 2007 than those on Catalina (Fig. 2). Arthropod biomass averaged 1.55 ± 0.31 mg of dry mass per gram of wet vegetation (n = 59) on Santa Cruz and 0.40 ± 0.06 (n = 58) on Catalina, a difference that was significant after controlling for sampling interval (two-way ANOVA, $F_{2,116} = 17.3$, $P < 0.0001$). The third sampling interval (see Fig. 2) also yielded significantly more arthropod biomass than the first and last ($F_{4,116} = 5.4$, $P = 0.0005$, Tukey's HSD), with no statistically significant interaction between island and sampling interval ($P > 0.05$). Most of the biomass during the breeding season was in the form of Lepidopteran larvae, the primary food item warblers feed to their nestlings (Sogge et al. 1994). Interestingly, this arthropod group made up a greater percentage of the total arthropod biomass on Catalina (65%) than it did on Santa Cruz (35%). Even so, the biomass of Lepidopteran larvae was nearly three times lower on Catalina (0.32 ± 0.06 mg/g vegetation, compared to 0.92 ± 0.23 on Santa Cruz). Warblers on Catalina did not compensate for the lack of food by defending larger territories. In contrast, their territories were much smaller on Catalina (0.11 ± 0.01 ha, n = 45) than on Santa Cruz (0.57 ± 0.10 ha, n = 18; t-test, $t_{61} = 10.2$, $P < 0.0001$) and they bred at higher densities (4.5 and 1.1 pairs/ha on Catalina and Santa Cruz, respectively), a pattern that is consistent with previous years (Ghalambor and Sillett, unpublished data).

Oak Growth

On Catalina, only 34% of oaks had grown new leaves by April (n = 158) and we found considerable spatial variation in the degree of leaf-out (Fig. 3). The orange-crowned warblers that built nests did so on territories where at least 40% of oaks had grown new leaves. At the same time, females on many territories with >80% oak leaf-out did not initiate nesting activities. Although data are not available for Santa Cruz to make a formal comparison, we observed that in 2007 nearly all oaks in the study area had grown new leaves by April (personal observation). This suggests that in contrast with Catalina, availability of new oak leaves were not a limiting factor on Santa Cruz.

DISCUSSION AND CONCLUSIONS

Our data indicate that *V. c. sordida* breeding on Catalina experienced a much stronger impact of the 2007 drought than did warblers breeding on Santa Cruz. Warblers on Catalina bred nearly a month later than those Santa Cruz, and only 11% of females built nests and only 2% laid eggs. No young fledged from our Catalina study plot in 2007. All females on the Santa Cruz plot, in contrast, attempted to reproduce, although few were successful because of high rates of nest predation. In the end, the reproductive output of warbler pairs was similarly poor on both islands (<1 young fledged per pair, on average).

The events of 2007 stand in stark contrast to previous years on Catalina. From 2003 to 2005, nests were initiated as early as February and as late as March, and on average, warbler pairs fledged >2 young per year (Ghalambor and Sillett, unpublished data). In the extremely wet year of 2005 (62 cm of rain during the preceding winter), at least 15% of females attempted second broods. The 2006 breeding season was relatively dry (21 cm) and the timing of reproduction was similar to that observed in 2007, although in that year all monitored females attempted to reproduce and some were successful in

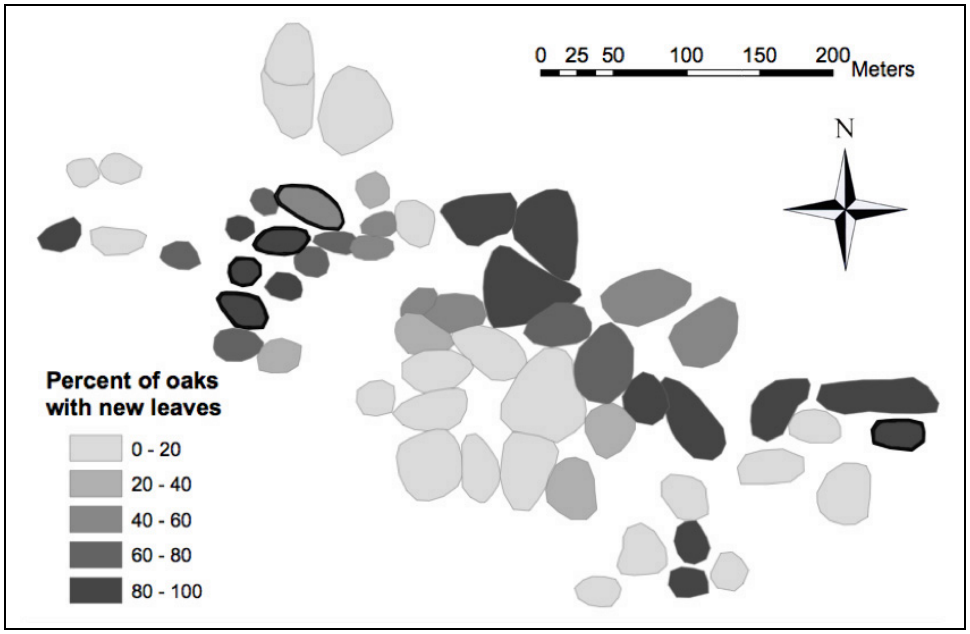

Figure 3. Spatial pattern of leaf growth for island scrub oak (*Quercus pacifica*) on the Santa Catalina Island study site in April 2007. Each polygon represents an orange-crowned warbler territory, and the shading denotes the estimated percentage of oaks that grew new leaves (see text). Nests were built on the territories outlined in black.

fledging young (0.7 young per pair; Ghalambor and Sillett, unpublished data). These patterns are consistent with a five-year dataset on rufous-crowned sparrows (*Aimophila ruficeps*) breeding in coastal sage scrub habitat on the California mainland. Bolger et al. (2005) reported a positive linear relationship between rainfall and reproductive output, which was attributed to a combination of limited food availability in drier years and reduced predation pressure in wetter years (Morrison and Bolger 2002). As in this study, they documented complete reproductive failure during the driest year.

The paucity of nesting attempts detected on Catalina in 2007 was not due to inconsistent survey effort. A four-person field crew has monitored the Catalina study site every year from 2003 to 2007, and two of the 2007 members had been part of the field crew in previous years (five breeding seasons combined experience). In addition, the field crew on Santa Cruz also consisted of four people and, in a much more challenging nest-finding environment, was still able to detect nesting activity for every focal pair. If anything, the data presented here for Catalina may be an overestimate of the proportion of females who attempted to breed on the island. Bulrush Canyon is among the wettest drainages on Catalina, and the study site is located within prime habitat on the canyon bottom. We found no warbler nests on a nearby xeric ridge plot, and that habitat type is much more common across the island (Knapp 2005; Yoon et al., unpublished manuscript).

Rainfall was low on both islands during the 2006–2007 drought, although Catalina received only 60% of the small amount of rain that fell on Santa Cruz (see Fig. 1). Our data indicate that this precipitation difference had a clear biological effect: the degree of oak leaf-out and the abundance of food were much lower on the Catalina study plot. We suggest that these environmental factors were instrumental in determining the timing and number of nesting attempts. Orange-crowned warblers depend on the availability of Lepidopteran larvae to feed young during the energetically demanding nestling period, and larvae during that time are primarily obtained from newly grown oak leaves (Ghalambor and Sillett, unpublished data). Warblers on Santa Cruz started building nests well before the peak in food abundance (see Fig. 2), indicating that some other factor—for instance, oak leaf-out—provided the necessary cue to signify food availability during the nestling period. On

Catalina, few oaks grew new leaves and those that did were concentrated in patchy areas. Warblers that built nests on that island had territories that were located in areas where >40% of oaks had leafed-out (see Fig. 3), and even then individuals did not have enough food resources to successfully raise their broods to fledging, as indicated by the one nest that failed due to starvation. The warblers that did not lay eggs, therefore, appeared to do so because of a lack of food.

Compared to Catalina, warblers on Santa Cruz had enough food resources to breed, but nest predation appeared to limit their reproductive output. Both islands have nest predators (e.g., gopher snakes *Pituophis melanoleucus*, island foxes *Urocyon littoralis* ssp., and deer mice *Peromyscus maniculatus* ssp.), but Santa Cruz is the only Channel Island with a visually oriented predator of songbird nests, the island scrub-jay. Only two warbler pairs were successful in raising a brood to fledging of the 18 pairs monitored, and the vast majority of nests failed due to predation (23 of 27). Top-down processes, therefore, appeared to be a primary factor that limited the reproductive success of warblers on Santa Cruz during the 2006–2007 drought. The high rate of nest predation did not differ significantly from that observed during the 2005 breeding season (Sofaer et al., unpublished data), which followed an exceptionally wet winter, so it appears as though top-down processes predominate on Santa Cruz regardless of rainfall patterns.

Nest predation is likely higher on Santa Cruz because of both direct predation by scrub-jays and indirect effects on nest-site placement. Mainland populations of *V. celata* are ground nesters; however, populations that breed on the Channel Islands exhibit plasticity in the height at which they place their nests (Sogge et al. 1994; Peluc et al. 2008). On Catalina, they frequently build nests in vegetation off the ground and can do so up to 8 m in height. This plasticity in nest placement appears to be adaptive because ground nests suffer from the highest predation rates on Catalina (Peluc et al. 2008). On Santa Cruz, in contrast, *V. c. sordida* typically build nests within 0.5 m of the ground (Ghalambor and Sillett, unpublished data). It appears as though this behavior is due to the presence of jays because (1) the vegetation used to build off-ground nests on Catalina (e.g., *Quercus, Rhus* spp.) is also present on Santa Cruz (Schoenherr et al. 1999), and (2) on Catalina warblers will build nests on the ground if they are exposed to an experimental jay presentation (Peluc et al. 2008). In addition to being a potential nest predator, therefore, scrub-jays may cause higher predation rates on Santa Cruz by inducing *V. c. sordida* to nest on or close to the ground, where they are at risk from mammalian and reptilian predators.

We note that the strategy of nesting lower in the presence of jays may have been rendered somewhat ineffective due to the presence of feral pigs (*Sus scrofa*) on the island. Pigs were introduced to Santa Cruz in the 1850s, and their rooting caused extensive damage to understory vegetation which in turn reduced the availability of concealed nesting sites for ground and shrub-nesting birds. Pigs were also likely predators of nests on the ground and in lower vegetation strata. By 2006, an eradication program had removed the pigs from the island (Morrison 2008), but drought conditions predominated between that time and the 2007 nesting season, so vegetation recovery was limited. It will be important to monitor warbler nest success in subsequent years, following rains and the recovery of understory vegetation, to assess whether rates of nest predation decline with the increase in understory structure.

Understanding biotic responses to climate variability and the relative importance of bottom-up versus top-down processes will be essential for predicting future impacts of climate change. Long-term projections for southern California point to a drying trend and increased variability in precipitation patterns (Cayan et al. 2008). Severe droughts such as the one experienced in 2006–2007, therefore, could be a more frequent occurrence in the coming century. We found substantial differences in the degree to which a severe drought affected *V. c. sordida* breeding on Catalina and Santa Cruz islands, along with the plants and arthropods upon which the warblers depend. Our results underscore the importance of comparative studies across the eight Channel Islands, particularly with regard to the factors that control phenology and limit productivity in terrestrial plants and animals.

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THE INFLUENCE OF NEST SUBSTRATE AND NEST SITE CHARACTERISTICS ON THE RISK OF SAN CLEMENTE SAGE SPARROW NEST FAILURE

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Abstract—Relatively small areas of critical habitat in island ecosystems can be essential to the survival and persistence of endemic threatened and endangered species. The San Clemente sage sparrow (*Amphispiza belli clementeae*) is a federally threatened, non-migratory subspecies endemic to San Clemente Island. During the breeding season, the population is limited to the lower marine terraces along the island's western shore. From 1999 through 2006, we located 870 San Clemente sage sparrow nests in 25 nest substrates; 73% of which were in boxthorn. We examined nest site characteristics that most influenced nest failure rates and compared nest survival among nest substrates and nest substrate types. The risk of nest failure varied annually and was significantly reduced when pairs nested in boxthorn and placed their nests near the center of the shrub. However, we found no significant differences in daily nest survival rates between boxthorn and non-boxthorn nest substrates and among nest substrate types. Three times as many nests were built in boxthorn as were built in all other substrates combined. These results suggest that the availability of boxthorn as nesting habitat may be an important factor driving the distribution and growth of the San Clemente sage sparrow population.

INTRODUCTION

Conservation of critical habitat for threatened and endangered bird species is essential for their long-term protection and management (Taylor et al. 2005). In some cases the habitat critical to the conservation of a species is not designated at the time of its listing because the species' habitat requirements are not adequately known. In these circumstances, it is crucial to determine those habitat features that are necessary to the long-term viability of the protected species.

The San Clemente sage sparrow (*Amphispiza belli clementeae*) is a non-migratory subspecies endemic to San Clemente Island (SCI), a U.S. military installation located off the coast of California. Once it was described as a common island resident (Grinnell 1897; Linton 1908; Howell 1917; Grinnell and Miller 1944; Miller 1968). However, following a 1976 estimate of 93 individuals (Byers 1976), concerns were raised about the long-term persistence of the San Clemente sage sparrow because of low population levels and limited distribution, severe habitat degradation by feral goats (*Capra hircus*), predation pressure from feral cats (*Felis catus*), and habitat loss and degradation due to invasive plant growth and human disturbance (U.S. Fish and Wildlife Service 1976). In 1977, the U.S. Fish and Wildlife Service listed the San Clemente sage sparrow population as a federally threatened subspecies, but did not officially describe their critical habitat (Greenwault 1977). Before potential management actions such as habitat restoration can be considered, it is important to characterize the habitat requirements of this species.

Essential bird habitat is often assessed in terms of the "quality" of the habitat to a particular life stage and most often refers to nesting habitat (Pidgeon et al. 2006). Willey (1997) was the first to describe the nesting habitat used by San Clemente sage sparrows in 1985, and he reported that they nested exclusively in boxthorn. However, his study was restricted to a single breeding season and his sample size was limited by a small population (Willey 1997). The Institute for Wildlife Studies

(IWS) has monitored the sage sparrow population on San Clemente Island since 1999, and has documented several other substrates used for nesting (Beaudry 2004; Kaiser et al. 2007). The objective of this paper is to determine the importance of boxthorn to successful reproduction and recruitment for the resident sage sparrow population. To achieve this objective, we utilized data from 1999 through 2006 to compare nest survival among different nest substrates. We also examine the influence of other nest site characteristics on the probability of nest failure. Examining the importance of nest substrates and characteristics of nest sites to successful reproduction will improve our understanding of the relationship between habitat preferences and suitability.

METHODS

Study Species

Sage sparrows are socially monogamous (Martin and Carlson 1998), but male polygyny is not uncommon and varies annually (Kaiser et al. 2007). Adults begin reproducing in their first year (Hyde 1985) and can attempt up to five nests in a breeding season (Stahl et al. 2008). The timing of territory establishment may depend on winter rainfall patterns, with establishment in late December after high rainfall totals and later in the season with drought conditions (Beaudry et al. 2003; Stahl et al. 2008). Breeding activity and breeding season length may also depend on rainfall, with peak activity occurring during March and April (Hyde 1985). During their breeding months, sage sparrows are mostly found on the lower marine terraces along the western shore of SCI in maritime desert scrub habitat. However, sage sparrows have been observed in small numbers on the central plateaus, along the eastern slope where a narrow band of maritime sagebrush (*Artemisia californica*) is found, and in canyons in woody shrubs (Hyde 1985; Kaiser et al. 2007).

Study Area

San Clemente Island (118° 30'W, 33° 00'N) is the southernmost of the California Channel Islands located approximately 92 km off the coast of California. The island is 14,764 ha in area extending 34 km north to south and between 2.5 and 6.5 km east to west. SCI is characterized by a series of marine terraces on the west side and a steep escarpment on the east side. The island experiences a Mediterranean dry summer subtropical climate with mild average mean summer and winter temperatures of 18°C and 13°C, respectively, with almost constant 8–24 km/h wind speeds. SCI receives an average of 13 cm of rainfall annually, mostly between December and April, and is often covered by heavy fog along the coastline.

The lower western and southern marine terraces of SCI are associated with the maritime desert scrub – boxthorn plant community. At lower elevations, maritime desert scrub habitat is dominated by boxthorn interspersed with snake cactus (*Bergerocactus emoryi*), island tarplant (*Deinandra clementina*), Australian saltbush (*Atriplex semibaccata*), California saltbush (*Atriplex californica*), coastal prickly-pear cactus (*Opuntia littoralis*), mixed grasses (*Avena* spp., *Stipa comata*, and *Hordeum jubatum*) and forbs, and lichen cover on shrubs (Kellogg and Kellogg 1994). At higher elevations, maritime desert scrub habitat is dominated by prickly pear and coastal cholla cactus (*Opuntia prolifera*).

The study region monitored by IWS extends along the western shore of the island and includes land cover that is predominantly the maritime desert scrub – boxthorn plant community (Fig. 1). In 1999, eight 12.5 ha study plots were established to monitor a portion of the sage sparrows on San Clemente Island (Munkwitz et al. 2000). Locations of the plots were based on documented habitat use by San Clemente sage sparrows (Hyde 1985; Willey 1990; KEA 1997), and plot sizes were dictated by dimensions of the marine terraces. In 2000, after sage sparrow nesting pairs were detected in areas they had not previously been known to occupy, the eight original plots were replaced with six larger plots ranging in size from 20 to 40 ha (Munkwitz et al. 2000). Three plots on the lower terraces covered the area monitored in 1999. In addition, two plots were located on mid-level terraces, and one plot was located on an upper terrace (Munkwitz et al. 2000). In 2002, the sampling design was adjusted according to improved knowledge of sage sparrow distribution and density patterns, adding one plot to the mid-level terrace and one plot to the upper terrace, and removing one plot from the lower

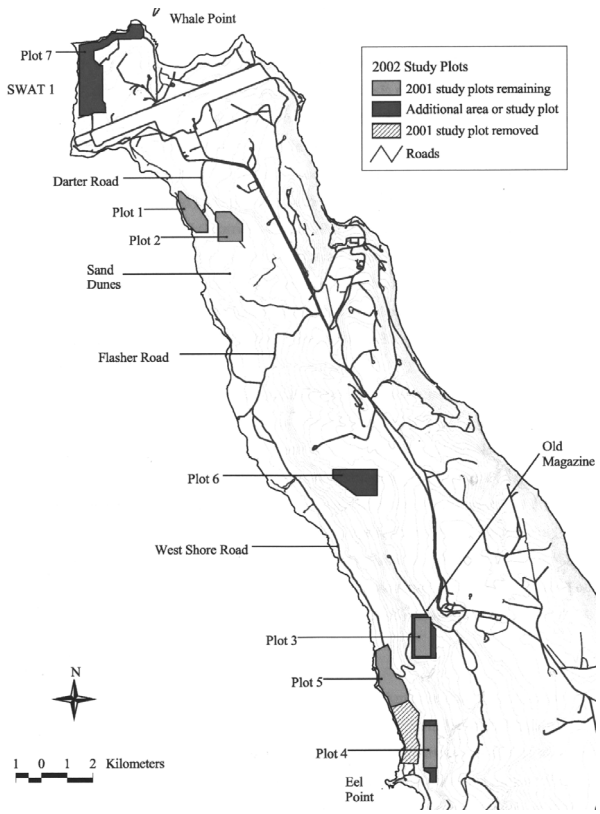

Figure 1. Location of the study plots searched for San Clemente sage sparrow nests on San Clemente Island, California. Plot boundaries from 2000–2001 (in gray) were refined in 2002 to include additional area (plots 3, 4, 6, 7, in black) and reduce area (plot 5, hatched).

terrace (Beaudry et al. 2003). The sizes of these plots ranged in size from 20 to 60 ha. The distance between two plots on the same terrace was 2–4 km, and plots on different terraces were 50 m apart. For six of the study plots we placed pin flags every 50 m in a grid system to facilitate nest searching. For the seventh plot, which was located in a military training range, we generated a map using a global positioning system receiver (GPS; Garmin eTrex Venture®, GARMIN Corporation, Olathe, KS) by marking landmarks such as boulders, posts, and fences.

Nest Monitoring

We searched for San Clemente sage sparrow nests in each established study plot throughout the breeding season (February – July) from 1999 through 2006. We located nests by observing behavioral cues such as adults carrying nesting material, food, or removing fecal sacs from nests, and followed incubating females returning to their nests (Martin and Geupel 1993). In addition, we located nests on an *ad hoc* basis outside of the plot boundaries while walking line transects surveyed as part of our larger monitoring project. We found most nests during the building and laying stages and estimated the age of each nest when it was found. If, however, a nest was found during the incubation or nestling stages, we estimated nest age by backdating using the average length of each nest stage calculated from previous years of data. We monitored nests every three to five days to determine the status of the contents, until the nest fledged or failed. We visited the nest more frequently during the fledging window and recorded a nest as fledged if a parent was seen with at least one young near the nest or if parents were behaving as if dependents were nearby (i.e., parents seen carrying food several times to one or more locations on the ground and reappearing without food; Ralph et al. 1993). We recorded a nest as failed if the nest was abandoned with eggs or nestlings in the nest or if the nest was depredated. We recorded a nest as depredated if the predation event was observed, if there was damage to the nest structure (e.g., nest torn out of substrate) with remains of eggs (e.g., broken eggshells) or nestlings, or if no parents were observed near the nest with fledglings and the nest was empty and intact (Ralph et al. 1993). If no adult behavior was observed and there was no evidence of predation or fledging at the nest site, we assigned the nest an uncertain fate. A nesting attempt was considered successful if at least one San Clemente sage sparrow fledged. We recorded locations of nests using a GPS receiver and marked them with flagging at a 5 m distance.

Nest Site Characteristics

From 1999 through 2006, we collected data on the primary species of plant supporting each nest (nest substrate). From 2000 to 2005, we measured eight additional characteristics of each nest site (height, distance to canopy, distance to center, distance to edge, substrate height, substrate width, vertical nest concealment, and horizontal nest concealment) after nests became inactive. Nest height, distance to canopy, distance to center, and distance to edge were respectively, the distance from the rim of the nest to the ground, top of shrub, center of the shrub, and nearest edge. Substrate height and width were height and maximum width

of the supporting nest substrate. We quantified nest concealment by visually estimating the percentage of the nest hidden through vegetation by standing 1 m in front of the nest from the four cardinal directions and from 1 m directly above the nest. We report vertical concealment as the amount of concealment from above. Horizontal concealment is the mean concealment among the four cardinal directions.

Statistical Analyses

The Mayfield method (Mayfield 1961, 1975) was used to estimate mean daily nest survival rates (DSR) during the incubation and nestling stages for each nest substrate species that supported greater than 15 nests (Table 1), which is the minimum sample size recommended for accuracy using Mayfield's method (Hensler and Nichols 1981; Hines and Sauer 1989). We terminated exposure (i.e., number of days during which a nest was observed) using Mayfield's midpoint approach for nests of known fate, which assumes that nests failed between nest check intervals (Mayfield 1975; Manolis et al. 2000). We used data collected from 1999 through 2006 to calculate the average length of the incubation stage (12 days) and the nestling stage (11 days). These averages were based only on nests that we found prior to the beginning of the stage and that successfully completed that stage in the nesting cycle. Nest survival rates (NSR) for the entire nesting cycle were calculated as the product of the stage survival rates (SSR) for the incubation and nestling stages. Standard errors and confidence intervals for Mayfield estimates were calculated according to Johnson (1979).

Our primary objectives were to determine whether nest survival was lower in boxthorn nests and whether nest substrate influenced nest failure rate. We used χ^2 tests in program CONTRAST (Hines and Sauer 1989) to determine whether boxthorn DSR were significantly different from all other nest substrates combined. Comparisons were made for the incubation and nestling stages separately and for the entire nesting cycle because Mayfield's method assumes constant survival over the entire nesting cycle, which is an assumption that is often violated and can lead to biased estimates (Manolis et al. 2000). It is not possible to examine factors that affect nest survival rates using Mayfield's method except for grouping the data by the different levels of the factor, which is limited by sample size. This approach restricts the examination of multiple potential factors influencing nest survival. Thus, we compared DSR among substrate types (e.g., woody shrub/sub-shrub, cactus, grass and forbs, non-woody shrub/sub-shrub; Table 1). We grouped nest substrates by these substrate types to utilize all nest substrate data in comparisons of DSR among vegetation that had similar characteristics for nest support, protection, and concealment. We chose to use Mayfield's method because DSR are widely reported and this allows for direct comparison with DSR of nesting sage sparrow subspecies on the mainland. We also report apparent nest success, which is the ratio of successful nests to total nests found.

With the eight-year nest site characteristics dataset, we used survival time analysis with Cox proportional hazards regression as an alternative to Mayfield's method to examine the influence of year, elevation, and nine nest site characteristics including nest substrate on the probability of daily nest failure rates (PROC PHREG; SAS Institute 2004). Mayfield's method has limited power to detect significant differences in statistical comparisons if the sample size of nests in each group is small, which results in wide confidence intervals and less robust estimates (Manolis et al. 2000; Hazler 2004). Thus, because the majority of sage sparrow nests were supported by boxthorn, we needed a more powerful analysis to detect potential differences in nest survival between boxthorn and all other nest substrates. We evaluated nest survival time (exposure days) as risk factors and included nest fate as a censor variable, where successful and uncertain nests were censored and failed nests uncensored. In this semi-parametric regression model there is no underlying distribution assumption and the hazard of any nest is a fixed proportion of the hazard for any other nest (Allison 1997). The hazard ratios are the effects of each nest site characteristic on the risk of nest failure. The hazard function is unspecified; therefore it is difficult to obtain actual estimates of daily nest survival (Hazler 2004), which is another reason why we report Mayfield's DSR estimates. Cox regression does not assume constant mortality and the response variable is exposure days, rather than nest fate (Manolis et al. 2000). Nests that are observed only during the incubation or nestling

Table 1. Species of vegetation that supported 870 San Clemente sage sparrow nests of known and uncertain fate on San Clemente Island, California, 1999–2006. We only included species that supported >1% of the nests in our sample. Thirty-one nests were built in substrates that represented <1% of the nests in our sample.

Species	Nest substrate type	*n*	Percent of total
Boxthorn (*Lycium californicum*)	Woody shrub sub-shrub	636	73.1
Island tarplant (*Deinandra clementina*)	Woody shrub sub-shrub	42	4.8
Island butterweed (*Senecio lyonii*)	Woody shrub sub-shrub	41	4.7
Grass (*Avena, Bromus, Hordeum, Nassella* spp.)	Grass and forbs	41	4.7
Snake cactus (*Bergerocactus emoryi*)	Cactus	20	2.3
Island morning glory (*Calystegia macrostegia amplissima*)	Woody shrub sub-shrub	20	2.3
Prickly-pear (*Opuntia littoralisi*)	Cactus	16	1.8
California wishbone bush (*Mirabilis californica*)	Non-woody shrub sub-shrub	13	1.5
Australian saltbush (*Atriplex semibaccata*)	Woody shrub sub-shrub	10	1.1
California saltbush (*Atriplex californica*)	Non-woody shrub sub-shrub	5	0.6
Silver birds-foot trefoil (*Lotus argophyllus argenteus*)	Non-woody shrub sub-shrub	4	0.5
Lupine (*Lupinus guadalupensis*)	Grass and forbs	4	0.5
Forb (Unknown spp.)	Grass and forbs	3	0.3
Russian thistle (*Salsola tragus*)	Non-woody shrub sub-shrub	2	0.2
Clover (*Trifolium* spp.)	Grass and forbs	2	0.2
Pineapple weed (*Amblyopappus pusillus*)	Grass and forbs	1	0.1
Sagebrush (*Artemisia* spp.)	Woody shrub sub-shrub	1	0.1
San Clemente Island milk-vetch (*Astragalus nevinii*)	Woody shrub sub-shrub	1	0.1
Island sunflower (*Encelia californica*)	Woody shrub sub-shrub	1	0.1
Fern (Unknown spp.)	Grass and forbs	1	0.1
(*Gnapthalium* spp.)	Grass and forbs	1	0.1
Leafy Malacothrix (*Malacothrix foliosa*)	Grass and forbs	1	0.1
Cholla (*Opuntia prolifera*)	Cactus	1	0.1
Threadstem (*Pterostegia drymarioides*)	Grass and forbs	1	0.1
Pickleweed (*Salicornia subterminalis*)	Non-woody shrub sub-shrub	1	0.1
Wirelettuce (*Stephanomeria* spp.)	Non-woody shrub sub-shrub	1	0.1

period are not given the same weight as nests observed throughout the entire nesting period. For the nest substrate variable, nests supported primarily by boxthorn were binary coded (1) and all other nest substrates were coded (2). Year, elevation, substrate width and height, vertical and

horizontal nest concealment, nest height, and nest distance to substrate edge, center, and canopy were entered as continuous variables. We excluded 44 nests with uncertain nest fates from the analysis to improve our ability to detect differences between successful and failed nests.

RESULTS

We monitored 870 sage sparrow nests on the seven study plots between 1999 and 2006. Of 307 failed nests, eight (3.7%) were abandoned after eggs failed to hatch and all of the remaining 209 (96.3%) nest failures were attributed to predation. Eighty-three nests were depredated during the incubation stage and 126 during the nestling stage. Apparent nest success was 75% over all years and the entire nesting cycle.

Between 1999 and 2006, sage sparrows were observed to nest in 25 nest substrates (Table 1). The range of the nest site characteristics measured between 1999 and 2006 was large, but the variation around the mean measurement for each variable was small (Table 2).

For each substrate with >15 observations, Table 3 presents daily survival rates for the incubation and nestling stages, as well as stage survival rates for the incubation stage, nestling stage, and nest survival rate for the entire nesting cycle. Mean daily survival rates of nests in all substrates combined were 0.982 ± 0.002 for the incubation stage and 0.981 ± 0.002 for the nestling stage. The incubation stage survival was 80%; the nestling stage was 81%; and the nest survival rate was 65% for all substrates combined (Table 3).

Results of the chi-square tests indicated that there were no significant differences in daily nest survival rates between boxthorn and non-boxthorn nest substrates for the incubation ($\chi^2 1 = 1.0$, $P = 0.32$) and nestling stages ($\chi^2 1 = 1.0$, $P = 0.33$), or for the entire nesting cycle ($\chi^2 = 1.8$, $P = 0.18$).

Results of the Cox regression model (Table 4) indicated that the risk of nest failure was significantly influenced by year ($\chi^2 = 11.3$, $P < 0.001$), nest substrate ($\chi^2 = 8.6$, $P < 0.01$), and the distance from the nest to the center of the nest substrate ($\chi^2 = 3.8$, $P = 0.05$). The hazards ratios (Table 4) suggest that nests built in substrates other than boxthorn were 1.14 times more likely to fail, the risk of failure increased the further from the center of the nest substrate the nest was placed, and failure rates differed among years.

DISCUSSION AND CONCLUSIONS

The nesting area of San Clemente sage sparrows was first described by Willey (1997) based on 31 monitored nests in a single breeding season. We collected measurements on 870 nests over an eight-year period and some of Willey's (1997) initial findings were supported by our data. However, we also gained new insights into the importance of boxthorn to the successful reproduction of sage sparrows on SCI.

While the nests that Willey (1997) found were built exclusively in boxthorn, we discovered that San Clemente sage sparrows are capable of greater flexibility in their choice of nest substrates. Although species other than boxthorn accounted for

Table 2. Means and standard errors of nest site characteristics of San Clemente sage sparrow nests on San Clemente Island, California, 1999–2006.

Variable	n	Mean ± SE	Range
Elevation (m)	713	46 ± 2	0–169
Nest substrate	815	-	-
Substrate width (cm)	662	383 ± 11	20–2200
Substrate height (cm)	664	55 ± 0.6	25–167
Vertical nest concealment (%)	649	67 ± 1	0–100
Horizontal nest concealment (%)	651	91 ± 1	18–100
Nest height (cm)	642	24 ± 0.3	7–69
Nest distance to substrate edge (cm)	648	46 ± 2	0–315
Nest distance to substrate center (cm)	601	67 ± 3	0–580
Nest distance to substrate canopy (cm)	641	25 ± 0.3	0–75

Table 3. Mayfield's daily nest survival rates (DSR), associated standard errors (SE), and stage survival rates (SSR) during the incubation and nestling stages, apparent nest success and the nest survival rates (NSR) of San Clemente sage sparrow nests on San Clemente Island, California for each nest substrate and substrate type, 1999–2006.

	Incubation stage		Nestling stage		Incubation and nestling stages				
Nest substrate	DSR ± SE	SSR (%)	DSR ± SE	SSR (%)	Nests with eggs or young	Nests lost	Nests with uncertain fate	Apparent nest success	NSR (%)
Boxthorn (*Lycium californicum*)	0.983±0.002	81.7	0.982±0.002	81.9	636	148	27	76.7	66.9
Island butterweed (*Senecio lyonii*)	0.995±0.005	94.6	0.982±0.007	81.5	41	8	0	80.5	77.1
Island tarplant (*Deinandra clementina*)	0.972±0.010	71.8	0.972±0.010	73.4	42	16	4	61.9	52.7
Grass (*Avena, Bromus, Hordeum, Nassella* spp.)	0.979±0.009	77.2	0.978±0.008	77.9	41	13	5	68.3	60.1
Snake cactus (*Bergerocactus emoryi*)	0.969±0.015	68.3	1.000±0.000	100	20	4	2	80	68.3
Island morning glory (*Calystegia macrostegia amplissima*)	0.963±0.018	63.4	0.978±0.013	77.9	20	7	3	65	49.4
Prickly-pear (*Opuntia littoralis*)	1.000±0.000	100	0.976±0.014	76.7	16	3	1	81.3	76.7
Total	0.982±0.002	80.5	0.981±0.002	80.9	870	217	44	75.1	65.1
Woody shrub/ sub-shrub	0.982±0.002	80.6	0.981±0.004	80.8	752	185	35	75.4	65.1
Cactus	0.981±0.009	79.5	0.989±0.006	88.8	37	7	3	81.1	70.6
Grass and forbs	0.982±0.007	80.0	0.973±0.008	74.3	55	18	5	67.3	59.1
Non-woody shrub/sub-shrub	0.983±0.012	81.7	0.974±0.012	74.3	26	7	1	73.1	61.1

just 25% of the nests we monitored, we found nests supported by 25 different plant species. The apparent increase in the number of nest substrates used by sage sparrows since Willey's (1997) study may have resulted from vegetation recovery after feral goats were removed in 1992. Another potential explanation for the increase in substrate use is that baseline data from Willey (1997) was spatially biased because study plots were restricted to habitat containing higher densities of sage sparrows and greater cover of boxthorn on the two lower marine terraces. Boxthorn density has been shown to be significantly lower on upper terrace plots compared to lower and mid-level study plots (Kellogg and

Table 4. Cox proportional hazards regression results examining the effect of elevation and nine nest site characteristics on the probability of daily nest failure rates in San Clemente sage sparrow nests on San Clemente Island, California, 1999–2006. In the regression model, the hazard for any nest is a fixed proportion of the hazard for any other nest.

Variable	χ^2	*P*-value	Hazard ratio
Year	11.3	<0.001	1.211
Elevation (m)	0.2	0.64	1.001
Nest substrate	8.6	<0.01	1.140
Substrate width (cm)	0.7	0.42	0.953
Substrate height (cm)	0.02	0.89	0.883
Vertical nest concealment (%)	0.2	0.67	1.002
Horizontal nest concealment (%)	0.9	0.36	1.008
Nest height (cm)	0.1	0.74	0.995
Nest distance to substrate edge (cm)	0.6	0.45	1.002
Nest distance to substrate center (cm)	3.8	0.05	1.003
Nest distance to substrate canopy (cm)	0.5	0.48	1.009

Kellogg 1994; Munkwitz et al. 2002). Our study design incorporated existing data on spatial variability in sage sparrow and boxthorn density, allowing us to sample all available habitats on the three terrace levels when the study plots were established. The difference in the number of nest substrates observed in Willey's (1997) study compared to ours may partially be explained by these density patterns. However, our data did not support the argument that these new nest substrates were used more frequently where boxthorn cover was lower at higher elevations.

Boxthorn had only the fourth highest Mayfield's nest survival rate following island butterweed, snake cactus, and prickly pear. However, there were no significant differences in comparisons of Mayfield's nest survival among nest substrates and the sample size of nests was low in the latter three substrates with 73% of the nests found in boxthorn. Island butterweed is a dense, leafy woody sub-shrub that is uncommon in high densities on the lower marine terraces along the western shore where sage sparrows breed (K. Klementowski, pers. comm.). Typically, island butterweed will leaf out in the spring and become dormant by mid-summer and lose its lower leaves (Hickman 1993), which would reduce its effectiveness at concealing nests later in the season. The nests we found in island butterweed became active during the first few months of the breeding season (January – April) in normal to wet years only. No nests were initiated in this substrate in the later months of the breeding season when its canopy cover would be reduced. Snake cactus and prickly pear are low, sprawling plants that grow in wide, tangled clumps. Snake cactus is protected by interlacing spines and prickly pear by very sharp narrow spines that may deter nest predators. While all three of these substrates do provide cover and protection from aerial and ground predators during nesting, they may not be as effective as boxthorn at concealing fledglings or providing immediate food resources (i.e., invertebrates, fruit) for nestlings, fledglings, and adults. However, cacti are interspersed throughout boxthorn habitat and nests built in cacti may benefit from proximity to boxthorn (Willey 1997), which is a spatial component that should be addressed in future research.

Among the substrate types, cacti had the highest Mayfield's nest survival rate followed by woody shrubs/sub-shrubs, non-woody shrubs/sub-shrubs, and grass/forbs. These results were consistent with the high nest survival rates observed in two cacti species and the woody shrub/sub-shrub results were likely driven by nests built in boxthorn, which made up the majority of the sample. Despite that nest survival rate was highest in cacti, this was not significant and sage sparrows nested predominantly in boxthorn. As mentioned previously, cacti may offer greater structural protection against predators compared to other substrate types (Hernandez et al. 2003).

In addition, we found that nest failure differed among years. However, it is difficult to interpret the hazard for each year separately because the Cox regression treats year as a continuous variable. Thus, it is not possible to compare estimates of nest failure rates among years. The timing of nest

initiation varies considerably among years, which is influenced by rainfall (Kaiser et al., in prep). Weather conditions likely influenced the availability of nest substrates and their effectiveness at concealment from predators and protection from inclement weather.

Our results comparing nest survival between boxthorn and non-boxthorn substrates differed between the Cox proportional hazard regression and Mayfield analyses. The chi-square analysis in CONTRAST indicated no significant difference in daily nest survival rates between boxthorn and non-boxthorn nest substrates for the entire nesting cycle, and no significant difference in daily nest survival rates among nest substrate types. However, the Cox regression analysis determined that the risk of nest failure was significantly greater for nests built in substrates other than boxthorn. There are three potential explanations for this finding. First, the sample sizes used in the Mayfield analysis included 44 nests that were not included in the Cox proportional hazard regression, which consisted of 16 nests in non-boxthorn substrates. These nests could have influenced the probability of nest failure in non-boxthorn substrates considering the low sample of nests found in non-boxthorn substrates.

We excluded nests with uncertain nest fates in the regression analysis to improve detection of biologically meaningful differences between successful and failed nests where nests with uncertain outcomes were censored from analysis (Hazler 2004). We did not exclude nests with uncertain nest fates in estimates of nest survival by Mayfield's method because the exclusion of nests with uncertain nest fates can lead to more biased estimates and influence statistical comparisons (Manolis et al. 2000). Second, Cox proportional hazard regression may be more sensitive to differences in nest survival and hence more powerful than comparisons of DSR because the assumption of constant mortality is relaxed. This is especially important considering that there may be seasonal influences on the selection of available nest substrate and differences in concealment in those substrates across the nesting cycle and season (e.g., island butterweed). Thirdly, differences in DSR among substrates may reflect low power of the Mayfield method rather than a true or biologically meaningful equivalence among substrates because of the wide confidence intervals for nest substrate types with only the minimum recommended sample size for analysis.

Several factors can potentially explain sage sparrow preferences in their selection of nesting habitat. The first is reduced predation risk. The nest survival rate of San Clemente sage sparrows, calculated at 65% for the years between 1999 and 2006, was much higher than that reported for similar subspecies on the mainland. Sage sparrows in central Oregon experienced nest survival rates as low as 17% (Rotenberry and Wiens 1989). The apparent nest success of San Clemente sage sparrows, calculated to be 75%, was also high compared to the 26% reported for mainland sage sparrows nesting in southern California (Misenhelter and Rotenberry 2000). San Clemente sage sparrows may have higher nest survival relative to the mainland subspecies because of a less diverse suite of potential nest predators. In central Oregon and southern California, snakes were the primary nest predator of mainland sage sparrows (Rotenberry and Wiens 1989; Misenhelter and Rotenberry 2000), but snakes were absent on SCI. Other predators not found on SCI that were implicated in nest failures on the mainland included long-tailed weasels (*Mustela frenata*) and chipmunks (*Eutamias spp.*) (Rotenberry and Wiens 1989). Moreover, San Clemente sage sparrows do not encounter brown-headed cowbirds (*Molothrus ater*) on the island, which were observed to be a major source of nest failure of sage sparrows nesting in southeastern Idaho and Washington (Reynolds 1981; Vander Haegen 2007). However, the island subspecies is vulnerable to predation by avian predators including the common raven (*Corvus corax*), American kestrel (*Falco sparverius*), San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*), barn owl (*Tyto alba*), and migratory raptors and owls. Potential mammalian predators include the feral cat, island fox (*Urocyon littoralis clementae*), black rats, and mice (*Peromyscus maniculatus* and *Mus musculus*) (Hyde 1985; USN 2002). Boxthorn habitat was thick, thorny, and likely more difficult to maneuver in, and the placement of nests within boxthorn shrubs where the vegetation was most dense may have provided maximal concealment and protection from predators.

Nesting in the center of the shrub may have offered protection from the wind, provided shading,

and reduced heat loss (Rich 1980). Willey (1997) demonstrated that sage sparrows on SCI placed their nests most often on the leeward side of boxthorn shrubs and suggested that their non-random nest placement would provide protection from the intense, prevailing winds that the west shore marine terraces regularly endure. Sage sparrows nesting in the Great Basin were sagebrush obligates and showed similar preferences in nest orientation (Peterson and Best 1985). Additionally, boxthorn acts as a substrate for insects, caterpillars, and spiders and produces seeds and berries throughout the breeding season (Hyde 1985). Thus, nesting in boxthorn may have provided a direct benefit by supporting a greater variety of food resources that could be acquired under concealment, necessary for the production of young (i.e., invertebrates and seeds), feeding of young and dependents (invertebrates) (Willey 1988; Martin and Carlson 1998), and surviving the molting period (i.e., fruit, invertebrates, and seeds) (Hyde 1985). Further, boxthorn offers numerous perches for singing males and enables females to enter their nests from any direction.

The condition and trend of SCI's plant communities between 1994 and 2003 were compared to baseline surveys conducted between 1992 and 1993 (USN 2004). Areas of SCI that were previously mapped as grassland or maritime desert scrub – grassland prior to goat eradication showed an increase in shrub cover after 1993 and was comprised of as much as 35% boxthorn (USN 2004). Maritime desert scrub – boxthorn habitat showed a maximum increase in boxthorn frequency of 35% (USN 2004). The increase in shrub cover appeared mostly at higher elevations in the southern part of the island (USN 2004) where goats were historically more abundant (USN 2002). Hence, although we do not know the pre-disturbed composition of vegetation prior to goats, the vegetation trends post eradication suggest that sage sparrow habitat has the potential to recover now that feral animals have been extirpated from the island. The change in ground and shrub cover in their nesting habitat could influence their preference for nest substrates. In addition, the availability of substrates may vary annually because of differences in yearly rainfall. Boxthorn, snake cactus, prickly pear, and island morning-glory were available as substrates in both wet and dry years, whereas, herbaceous plants such as island tarplant, island butterweed, and grasses did not grow or did not survive long in years with lower rainfall (Kaiser et al. 2007).

In conclusion, San Clemente sage sparrows overwhelmingly built their nests in boxthorn and 25 new substrates were documented for nesting since Willey's (1997) earlier study. Although nest predation was considerably low for this population compared to mainland subspecies, the risk of nest failure was significantly reduced when pairs nested in boxthorn and placed their nests near the center of the shrub. These results suggest that the availability of boxthorn as nesting habitat may be an important factor driving the distribution of the population across the island. Hence, the expansion of the population during the breeding season to habitat on the island not containing boxthorn is uncertain. However, we have observed seemingly suitable habitat that has remained largely unoccupied on the island across years when density and population levels have fluctuated (Kaiser et al. 2007). But given the importance of boxthorn to successful breeding, maritime desert scrub – boxthorn habitat should be evaluated further and protected as essential to the long-term persistence of this species.

We recommend exploring the factors affecting habitat use and dispersal to better understand the differences in foraging benefits and predation risk between boxthorn habitat and other available habitat dominated by cactus and grasses. This information will be especially important if habitat restoration becomes a necessary management consideration to offset increasing military use of maritime desert scrub – boxthorn habitat. Given the effect of year on nest failure rate, the influence of annual rainfall and temperature on the availability of nest substrates and nest failure among nest substrates should be investigated. Finally, we recognize that a species may require several habitat types for different stages of their life cycle and that breeding habitat requirements cannot fully be determined from nest site characteristics alone (Anders et al. 1998; Cohen and Lindell 2004). We advise investigating how habitat associations may differ during the fall and winter and examining mortality risks during these stages of their life cycle.

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BENEFITS OF SUPPLEMENTAL FEEDING ARE CLIMATE DEPENDENT IN THE SAN CLEMENTE LOGGERHEAD SHRIKE

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Abstract—Supplemental feeding is a key component to many conservation efforts. Because the effect of feeding on a target population's breeding biology interacts with weather in complex ways, supplemental feeding programs may be more influential on target populations in some years than in others. We examined the effect of supplemental feeding on breeding characteristics of San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) during both relatively dry and wet years. From 2001 through 2007, the mean number of independent young produced by supplementally fed shrike pairs was 30% higher than for non-supplementally fed pairs. Shrike breeding phenology was affected by both rainfall and supplemental feeding, with the beneficial effects of supplemental feeding most evident in dry years. In dry years, supplementally fed pairs initiated breeding an average of 12 days earlier, were nearly a third again as likely to renest after successfully fledging young, and attempted a third again as many nests as non-fed pairs. None of these effects were observed following relatively wet winters. Supplemental feeding did not affect nest success, nor did it result in a statistically significant increase in independent young production regardless of winter rainfall. These observations indicate that supplemental feeding reduces the negative impacts of food limitation imposed by periodic drought, but does not mitigate predation pressure on nesting shrikes. Our study suggests that supplemental feeding efforts should vary from year to year based on winter rainfall, with greater efforts put forth in drought years than during relatively wet years. This study demonstrates that evaluating the effects of provisioning on breeding components can provide a sensitive indicator of whether or not a program is working and that understanding the proximate mechanisms through which supplemental feeding acts is an important step to optimizing adaptive management of endangered species.

INTRODUCTION

Release programs that place captive-reared birds into the wild have been an essential technique in the recovery of several endangered species (Nesbitt and Carpenter 1993; White et al. 2005). Food supplementation to help newly released individuals adjust to their environment is a component of many soft release programs (Castro et al. 2003; Kreger et al. 2005). In addition, supplemental food provisioning can augment reproductive output of wild-born individuals, and is thought to buffer populations from the threat of extinction due to environmental stochasticity (Kuehler et al. 2000; Schoech et al. 2007).

Because food limitation can have negative effects on population growth, supplementation can be an effective management tool when nutritional resources are limiting. This is most evident during the energy-intensive breeding season (Martin 1987). For example, reduction of arthropod populations during a drought year curtailed reproduction in four resident bird species inhabiting coastal sage scrub in southern California (Bolger et al. 2005). On the Channel Islands, the San Clemente sage sparrow (*Amphispiza belli clementeae*) exhibited reduced reproductive effort in drought years (Kaiser et al. 2008) when plant productivity was greatly reduced (Beaudry et al. 2004). Drought-driven changes in resource abundance can impose strong selection pressure on birds (Grant and Grant 1995; Van Noordwijk et al. 1995; Visser et al. 1998).

Food supplementation has been associated with greater reproductive output through a variety of mechanisms, including earlier egg laying, increased

clutch size, egg volume, increased nesting attempts and nest success, and reduced intervals between clutches (Martin 1987; Robb et al. 2008). The effect of supplemental feeding on reproductive output may interact with variation in weather patterns and predation pressure in complex ways (Schultz 1991; Zanette et al. 2006; Preston and Rotenberry 2006). Consequently, proper implementation and evaluation of a supplemental feeding program depend on understanding the mechanism(s) through which feeding affects reproductive output.

In this paper, we examine the effects of supplemental feeding on the breeding characteristics of the San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*; SCLS). Endemic to San Clemente Island, California, the wild population of this endangered subspecies declined to 14 individuals by 1988, likely due to habitat degradation and exacerbated predation by non-native species (Scott and Morrison 1990; Mader et al. 2000). Since then, the U.S. Navy established a multifaceted recovery program including intensive monitoring of wild birds, control of non-native predators, habitat restoration, captive breeding, population augmentation with captive-bred birds, and supplemental feeding of captive-bred birds in the wild. The wild shrike population has increased substantially since 2000. This recovery has been fueled, in part, by high reproductive rates; shrike pairs in the wild have averaged > 2.5 fledglings per pair per year from 2000 through 2007 (Bradley et al. 2007). Reproductive rates have been greater in relatively wet years, and bolstered in dry years by breeding season supplemental feeding in combination with rat (*Rattus rattus*) control (Heath et al. 2008).

The mechanisms through which supplemental feeding affects shrike fecundity, however, remain poorly understood. In particular, optimal allocation of future feeding efforts depends on whether supplemental feeding acts through mechanisms that mitigate predation pressure or mechanisms that mitigate resource limitation. If supplemental feeding helps to mitigate predation pressure, by increasing nest survival or reducing the time it takes for a pair to renest after nest failure, future efforts might be better aimed at feeding pairs that do not receive predator protection. If supplemental feeding mitigates resource limitation, by promoting earlier nesting, more nesting attempts per season, or increasing renesting after successful attempts, future efforts might be best applied during drought years when resources are most limiting. Here we attempt to identify the mechanism or mechanisms though which supplemental feeding affects shrike fecundity. Because shrike reproduction is known to vary with rainfall (Heath et al. 2008), we also examine the data set for potential interactions between feeding, reproduction, and pre-breeding season precipitation. Although interactions between predation pressure and supplemental feeding may be as important as interactions between supplemental feeding and rainfall (Zanette et al. 2006; Preston and Rotenberry 2006), we do not examine these because supplemental feeding was associated with predator protection at sites and because we do not have accurate indices of predation pressure.

Study Species

SCLS are year-round residents of San Clemente Island, California. They are socially monogamous, and both male and female participate in nest building and in feeding and caring for young. Adults begin reproducing in their first year and have, on average, two broods per breeding season (Bent 1950). If initial nests fail, they can renest multiple times within the same breeding season (Yosef 1996). The breeding season begins with the forming of pairs at breeding territories, typically in February or March, and ends when the last broods fledge and young reach independence, typically in June and July (Bradley et al. 2007). Breeding territories are usually located in canyons where trees and shrubs provide nesting cover. Shrikes nest in a wide variety of plants and artificial substrates, but most nests are placed in island cherry (*Prunus lyonii*) or lemonade berry (*Rhus intergrifolia*) trees (Bradley et al. 2007).

Study Site

San Clemente Island lies 92 km west of the southern California coast. It is 148 km^2, making it the fourth largest of the Channel Islands. It has an arid climate, with a mean annual rainfall of 13 cm. Rainfall varies strongly both within and between years. Most precipitation falls between October and March. Because most rain falls over winter, spanning calendar years, bio-year accumulation (July–June) is more informative than annual

(January–December) rainfall in capturing relevant annual variation. Bio-year accumulation ranged from 3.8 to 40.9 cm between 2001 and 2007 (CS Northridge San Clemente Island Monitoring Project 2009). Plant phenology is closely tied to winter rainfall, with many plants failing to leaf out or flower in dry years (Beaudry et al. 2003, 2004). Drought years are also correlated with lower indices of rodent abundance on the island (Biteman et al. 2009).

The west side of the island has gentle sloping marine terraces covered in coastal scrub, and is cut by deep canyons that support a variety of tree and shrub species. The main plateau is dominated by grasslands with a regenerating cover of coyote brush (*Baccaharis salicifolia*). The eastern slope is steep, rugged, and covered with a mixture of grasses, coastal scrub, trees, and shrubs. Common tree and shrub species include oak (*Quercus tomentella*, and *Q. chrysolepsis*), island cherry and ironwood (*Lyonothamnus floribundus*), lemonade berry, toyon (*Heteromeles arbutifolia*), and sage (*Artimisia* sp.).

METHODS

We examined the effect of supplemental feeding on SCLS reproduction by comparing breeding characteristics between pairs that were supplementally provisioned prior to and during the breeding season and pairs that were not fed prior to or during the breeding season. Most supplementally fed birds were captive-bred and subsequently released onto SCI. The Institute for Wildlife Studies has carried out releases since 1999, using a variety of soft release techniques (Garcelon and Sharpe 1998; Fidorra et al. 2008). Generally, releases were carried out by transporting birds as single adults, paired adults, or in juvenile flocks to a release site where, depending on their breeding status, they were held in aviaries for several days to two months. Supplemental food was then provided at release sites through the remainder of the breeding season.

After release, adults and fledglings were fed at the site twice a day for the first three days, once a day for the next two weeks, then every other day until October when they were weaned to a 10-day feeding interval to encourage self-foraging (Fidorra et al. 2008). If birds remained at the release sites beyond the first breeding season, they were fed once every 10 days year-round unless they had nestlings in a nest, at which point they were fed once every three to five days. On occasion, wild-born birds formally mated to released birds still living near release sites were provisioned in the same manner. Consequently, both provisioned and non-provisioned sites were utilized by wild-born, captive-born, and mixed-origin pairs.

Food was delivered to shrikes in one of two ways. At sites easily accessible from the central plateau, food was placed in a shaded dispenser raised 1.5–2 m off the ground on a metal post (Fig. 1a). At sites located in less accessible canyon bottoms, food was placed in a plastic tub, which was

a)

b)

Figure 1. Photographs of supplemental feeding devices a) above canyon rims and b) for canyon bottom territories (photos courtesy A.-M. Easley).

delivered to the SCLS via a zip-line and pulley system (Fig. 1b). Once delivered, feeding behaviors were observed for 30 min and the numbers of food items eaten, fed to mates or nestlings, or cached were recorded. Food provided included live mice (*Mus musculus*), mealworms (*Tenebrio molitor*), and crickets (*Acheta domestica*). The amount that each shrike received was equivalent to 25–75 crickets and 25–75 mealworms, plus one to three mice per shrike per visit. When a pair had nestlings, the amount of crickets and mealworms provided was increased based on the number of nestlings in the nest. Live mice remaining after the observation period were removed so as not to attract shrike predators or competitors such as feral cats (*Felis catus*), kestrels (*Falco sparverius*), or common ravens (*Corvus corax*).

Breeding data were collected by biologists from Point Reyes Bird Observatory Conservation and the Institute for Wildlife Studies for every known SCLS pair on SCI from 1997 through 2007. During the non-breeding season, all known active and historic shrike territories were visited every 2–8 weeks, depending on accessibility. During the breeding season, territories were visited at least once a week, depending on nesting stage. During most visits, behavioral observations were made through spotting scopes from a distance of at least 100 m from nesting sites. Observation locations were chosen so that observers could see adult behaviors at or near the nest without disturbing the birds. Breeding status was inferred from observed behaviors (Scott and Morrison 1990). A nest was included in our sample if egg-laying behavior was observed. After hatching behavior was observed, nests were visited twice; once to count and age nestlings, and a second time to band nestlings when they were 9–11 days old. Birds were banded with United States Fish and Wildlife Service bands and a unique combination of three color bands. The vast majority of shrikes in the population could be uniquely identified by their color-band combinations.

Statistical Analyses

We compared estimates of reproductive parameters in wet years and in dry years between pairs that received supplemental food and those that did not, and examined interactions between feeding and rainfall. Specifically, we asked if supplemental feeding affected nest success (the probability that nests containing at least one egg subsequently produced at least one independent young), the onset of breeding (the date when a pair's first nest was initiated), renesting interval (the number of days between nest failure and egg hatching in the next nest attempt), and probability of attempting multiple clutches (the probability that a pair attempted an additional clutch after fledging young from their previous nest attempt).

We combined pairs from 2001 through 2007 for models comparing supplemental feeding. We excluded from our analysis sites that had the same pair of adults as the previous year ($n = 25$) to avoid the possibility that inter-annual mate fidelity might confound indices of reproductive success.

We used ANOVA (proc GLM SAS 8.0 SAS Institute Cary, NC) to analyze effects of feeding treatment and rainfall on clutch initiation date, time between nest attempts, and number of independent young. For each analysis, we nested feeding treatment within year and year within rainfall category. To check for interactions between weather and supplemental feeding and still account for the nested structure, we analyzed the difference between the value for each response variable at a site and the mean value for that variable for that year (hereafter, "annual residuals") and analyzed the effects of rainfall, supplemental feeding, and their interaction with an ANOVA. If the interaction term was significant at the 0.10 level, we subsequently compared feeding treatments separately for wet and dry years.

Because renesting probability, the number of nest attempts, and nest success could take on only a small number of values, they should be evaluated using logistic regression rather than ANOVA. However, preliminary analyses revealed that the nested structure used above made the results of logistic regression analysis difficult to interpret. To simplify interpretation, we conducted separate analyses for the effect of provisioning in wet and dry years on the annual residuals of these variables, which have a more continuous distribution. We applied an arcsine transformation to annual residuals of the two probabilities before analysis (Sokal and Rohlf 1995).

We did not use the standard Mayfield (Mayfield 1961) index to analyze nest success because our intensive monitoring throughout the year resulted in

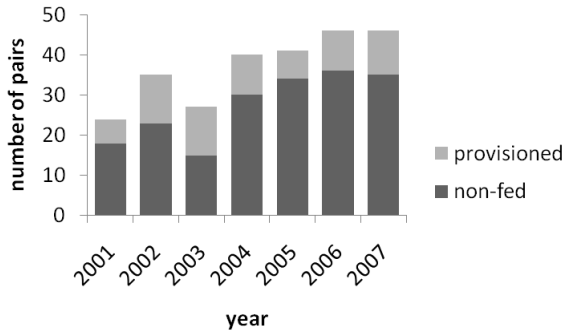

Figure 2. Number of breeding shrike pairs on San Clemente Island 2001–2007. Each bar represents the number of provisioned (light) and non-fed (dark) pairs known to have attempted at least one nest that year.

a very low chance that we failed to find nests before they failed. Before conducting analyses we reviewed data for normality and observed no significant deviations except as noted above.

The number and proportion of pairs that were supplementally fed varied year to year (Fig. 2). Wet years were defined as those with at least 100 mm rainfall during the winter months prior to the breeding season (November to February), and dry years as those with less than 100 mm rain in the same period. This cutoff point was chosen based on the large difference in breeding behaviors observed in another San Clemente endemic, the San Clemente sage sparrow, above and below the 100 mm winter rainfall threshold. We categorized 2001, 2003, and 2005 as wet years with 177 mm, 111mm, and 167 mm of annual rainfall respectively; and 2002, 2004, 2006, and 2007 as dry years with annual precipitation ranging from 34 to 40 mm.

For each comparison, we included breeding pairs comprised of individuals that had been in the wild for at least one winter. We excluded same-sex pairs, pairs for which egg-laying was never confirmed, and pairs where one or both individuals had been released from captivity that breeding year. To account for varying degrees of predator control effort from site to site (Cooper et al. 2005), only pairs that nested at breeding territories protected by both rodent poisoning and trapping were considered in analyses of reproductive success. Furthermore, we excluded nests from analyses of first clutch initiation date or post-failure renesting interval if the timing of visits to the breeding site did not allow us to confirm the date of egg-laying or nest failure to within five days of accuracy. Sample sizes for each of the treatment groups can be found in Table 1.

Table 1. Sample sizes used to analyze the effects of supplemental feeding on breeding components in relatively wet and dry years.

	Provisioned		Not provisioned	
Breeding component	Wet	Dry	Wet	Dry
Clutch initiation	19	23	45	86
Post success renesting probability	15	19	39	53
Number of nesting attempts	22	27	53	96
Post failure renesting interval	6	10	19	19
Nest success	22	27	53	96
Independent juvenile protection	22	27	53	96

RESULTS

Birds began nest building as early as January 17, and there was significant annual variation in the start of the breeding season, which was not related to winter rainfall (Fig. 3; Table 2). Within years,

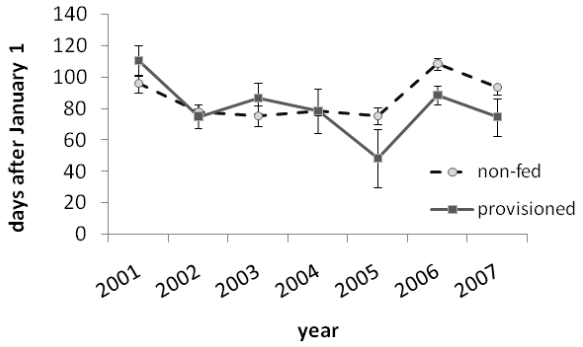

Figure 3. Annual variation in breeding dates. The average day of the year that pairs initiated nest building of their first nest attempt and whether or not they were provisioned from 2005–2007. Error bars represent +/- 1 standard error.

Table 2. Results from nested ANOVA analyses.

	Rainfall		Year		Provisioning	
Response variable	F	p	F	p	F	p
Clutch initiation	0.31	0.578	7.56	<0.001	2.11	0.046
Post failure renesting interval	0.31	0.581	1.11	0.368	0.78	0.605
Independent juvenile production	3.76	0.054	2.61	0.026	0.45	0.869

provisioned pairs tended to start nest building before unfed pairs, especially in the latter half of the study (Fig. 3; Table 2). There was a rainfall by provisioning interaction ($F_{1,169}$=3.35, p=0.07) such that provisioned pairs began nesting an average of 12 days earlier than non-fed pairs during dry years ($F_{1,107}$=4.88, p=0.03), while provisioning did not affect clutch initiation during wet years ($F_{1,62}$=0.37, p=0.55). A post-hoc comparison between earlier (2001–2004) and later (2005–2007) years of the study did indicate a significant interaction between time-period and effect of provisioning on breeding season initiation date ($F_{1,169}$=11.68, p<0.001), with a significantly positive (i.e., earlier initiation) effect in the latter ($F_{1,83}$=12.12, p<0.001) but not earlier ($F_{1,86}$=1.43, p=0.24) periods.

The average time between nest failure and hatching date of the following nest attempt was 27.25 (+/- 1.75 sem) days. Neither supplemental feeding nor rainfall impacted the amount of time pairs needed to renest following nest failure (Table 2), nor was there a significant rainfall by feeding interaction ($F_{1,50}$=1.15, p=0.221).

Whether or not a pair renested after successfully fledging young was positively influenced by supplemental feeding in dry but not wet years (Fig. 4a, dry years: $F_{1,70}$=5.35, p=0.023; wet years: $F_{1,52}$=0.20, p=0.658). In the absence of provisioning, shrikes were only 37% as likely to renest after fledging young in dry years as they were in wet years. In contrast, provisioned birds were nearly equally likely to renest regardless of rainfall. As a consequence, provisioned birds attempted a third again as many nests as non-fed pairs in dry years (Fig. 4b, dry years: $F_{1,121}$=9.94, p=0.002; wet years: $F_{1,73}$=0.31, p=0.581).

Nest success averaged 54% among predator protected sites and did not differ significantly between wet and dry years or between provisioned and non-fed pairs (Fig. 5, weather: $F_{1,126}$=0.11, p=0.746; supplemental feeding $F_{1,126}$=0.20, p=0.6334; weather x feeding interaction: $F_{1,126}$=0.16, p=0.687).

There were more independent young produced in wet than in dry years (Fig. 6; Table 2). Although there was a trend toward greater production of young at provisioned sites, the difference was not statistically significant (Table 2) and there was no rainfall by feeding interaction ($F_{1,194}$=0.02, p=0.891).

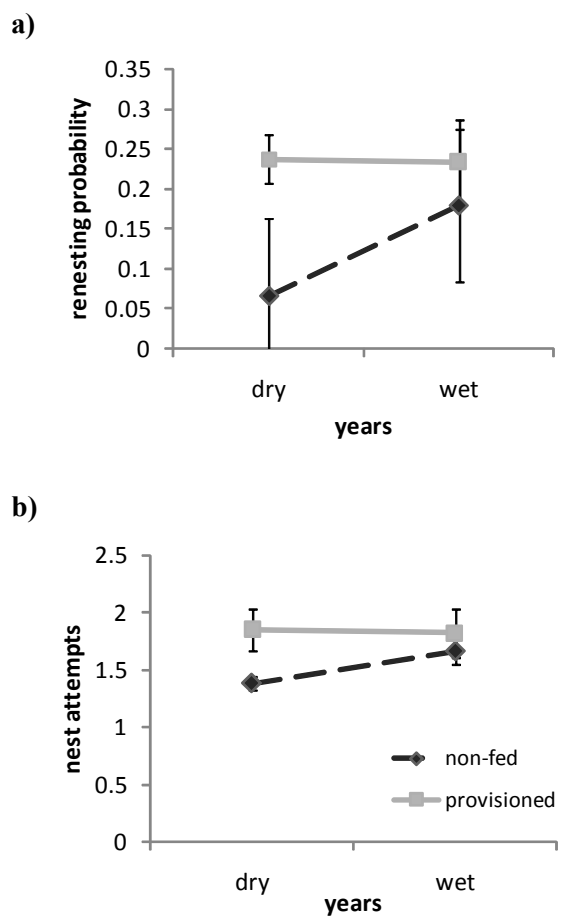

Figure 4. Effect of supplemental feeding on nest attempts. Supplemental feeding increases both a) the probability of renesting after successful nest attempt and b) the total number of nest attempts in a breeding season during dry but not wet years. Error bars represent +/- 1 standard error.

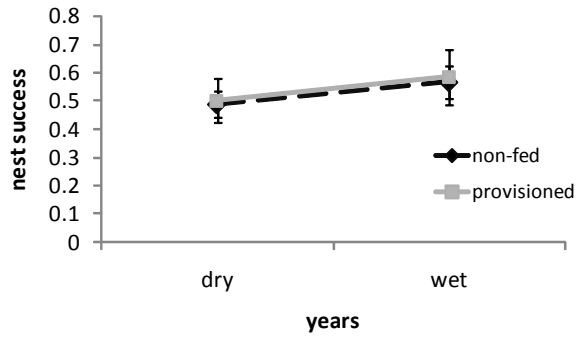

Figure 5. The probability that a nest produces at least one independent young did not differ between wet and dry years or between provisioned and non-fed pairs. Error bars represent +/- 1 standard error.

DISCUSSION

Provisioning promoted earlier breeding and increased the chance that pairs produced multiple clutches. These effects were most apparent during relatively dry years, and weak or nonexistent during relatively wet years. We did not find evidence that supplemental feeding affected either nest failure rates or the interval between nest failure and subsequent renesting attempts. These results suggest that supplemental feeding reduced the impacts of resource limitation but not the impacts of nest predation.

These results corroborate research that food can be limiting to reproductive success in temperate regions (Martin 1987), despite contrary arguments suggesting that birds can adapt to food scarcity (Ettinger and King 1980; King and Murphy 1985), or that the energy requirements of birds are less than environmental resource availability (Rotenberry 1980; Rosenberg et al. 1982). We found evidence that food limits both the timing of clutch initiation and numbers of clutches a pair can attempt in a season. Similar results by Aparicio and Bonal (2002) found a relationship between body condition and commencement of breeding. Earlier clutch initiation is often advantageous because it enables the production of offspring at a time of year when food is more abundant, resulting in increased fledgling survival (Korpimaki and Wiehn 1998; Preston et al. 2006; but see Verboven et al. 2001). Earlier clutch initiation also leads to increased fecundity by promoting increased breeding attempts (Nol and Smith 1987).

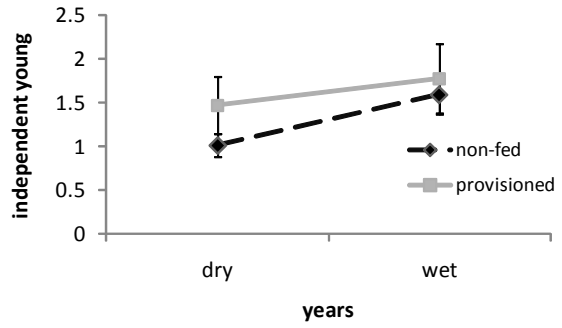

Figure 6. Number of independent young produced. The number of independent young produced per breeding shrike pair was not significantly different between wet and dry years or between provisioned and non-fed pairs. Error bars represent +/- 1 standard error.

Even for early breeders with a sufficiently long breeding season, the production of multiple broods depends on a bird's energy reserves (Martin 1987). For example, in great tits (*Parus major*) double brooding was influenced not by how early first nests were complete but by the abundance of caterpillars after the first clutch was completed (Verboven et al. 2001). Consequently, supplemental feeding may increase the number of nest attempts (Nagy and Holmes 2005; Zanette et al. 2006) by providing quality energy resources late into the breeding season. Although the number of clutches produced during a breeding season greatly influences overall production (Morrison and Bolger 2002; Nagy and Holmes 2005), this is one of only a few studies that have examined whether supplemental feeding increases the probability of multiple brooding or numbers of nesting attempts (Verboven et al. 2001; Zanette et al. 2006), and fewer have demonstrated an effect (Zanette et al. 2006).

In the California Channel Islands and Gulf of California islands both primary productivity (Beaudry et al. 2003, 2004) and small herbivore abundance (Polis et al. 1997) are closely tied to rainfall. In relatively wet years, resources are abundant as insects respond quickly to winter plant flushes after winter rains, and rodenticide consumption at protected sites indicate that rodent populations respond within a few months (Biteman et al. 2009). In contrast, during dry years many plants fail to even leaf out (Beaudry et al. 2003), insect populations crash (Polis et al. 1997), and rodents are scarce (Biteman et al. 2009). This annual variation in natural resources corresponded with the

observed interaction between rainfall and supplemental feeding. The lack of effect of supplemental feeding on the components of breeding associated with resource limitation is consistent with a "saturation effect," whereby provisioning only benefits a population when resources are relatively low (Schulz 1991). The saturation effect we observed associated with relatively wet years suggests that resources are not limiting shrike reproductive effort except during drought years. It further implies that provisioning wild birds is most beneficial during dry years, and will have little impact on the population during relatively wet ones.

As it is currently implemented, supplemental feeding does not influence those aspects of breeding impacted by predators. Supplemental feeding has been demonstrated to increase the protection of nestlings and fledglings in other species (Martin 1992) by increasing the amount of time available to adults for anti-predator behavior (Rastogi et al. 2006). An increase in nest attendance by provisioned adults (Arcese and Smith 1988; Wiebe and Bortolotti 1994; Dewey and Kennedy 2001; Nagy and Holmes 2004) has been shown to reduce overall nest predation (Yom-Tov 1974; Hogstedt 1981). Supplemental feeding may indeed benefit shrike nests in this way but go undetected because of the association of supplemental feeding and predator protection at shrike nesting sites. For example, lower predation pressure associated with predator protection might reduce the influence of supplemental feeding on predator-mediated breeding traits (i.e., nest success, post-failure renest interval) in the same way higher resource abundance reduced the effect on associated traits (e.g., clutch initiation date, probability of producing multiple clutches, and number of nest attempts). If so, our study design, imposed by the shrike recovery program, would likely miss any influence of supplemental feeding on predator-mediated breeding variables. However, the only previous experimental manipulations controlling both feeding and predation pressure suggest that supplemental feeding acts independently (Preston and Rotenberry 2006) or synergistically (Zanette et al. 2006) with reduced predator control; a saturating effect of predator control on the potential benefits of supplemental feeding has not yet been published.

Like Heath et al. (2008), we did not find a statistically significant effect of provisioning on independent young production, though there is a non-significant trend of greater production among provisioned compared to non-fed pairs. It should be noted that we used the same data as Heath et al. (2008) with the addition of nests from 2007. Part of the reason we did not detect a significant effect may be that we did not simultaneously control for the relatively large impact of other variables influencing production (Heath et al. 2008) such as whether the adult female was wild or captive born (wild females produced more young) and male age (older males produced more young). Since parent age and female origin were well mixed among treatments, they were unlikely to bias our results, but do introduce sources of variability in independent young production that reduce our power to detect the effects of provisioning. Another contributing factor may be that even though provisioned pairs attempt more nests in a breeding season, nest success was lower with each subsequent nest attempt (Institute for Wildlife Studies, unpublished data).

Using the effects of provisioning on breeding components to evaluate the efficacy of supplemental feeding programs has two advantages. First, because there is a more direct link between the two, the breeding components will be a more sensitive indicator than young production of whether or not a program is working. Second, understanding the mechanism(s) through which supplemental feeding acts is an important step to optimizing conservation efforts through adaptive management. For example, our study suggests that supplemental feeding efforts should vary from year to year based on winter rainfall, with greater efforts put forth in drought years; while resources may be better devoted to other programs (e.g., greater nest protection) during relatively wet years.

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BIOLOGICAL CONTROL AND ERADICATION OF FERAL HONEY BEE COLONIES ON SANTA CRUZ ISLAND, CALIFORNIA: A SUMMARY

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Abstract—After 1880, feral colonies of European honey bees (*Apis mellifera*) spread over all of Santa Cruz Island, though never invading any of the other northern Channel Islands. In line with other exotic animal removal programs (e.g., cattle, sheep, pigs), we outlined a program in October 1987 to eradicate all honey bee colonies on that island. That project evolved through four phases: 1) mapping and eradication of many colonies on the eastern half of the island (1988–1993), 2) introduction of a parasitic mite as a biological control (1994–1998), 3) monitoring residual honey bee activity (1999–2004), and 4) continued monitoring and certification of honey bee absence (2005–2008). We located the last known feral colony at the top of the Matanza grade on August 6, 2002 and found that same colony dead on March 31, 2003. The number of target foraging sites visited by honey bees declined steadily through the years, with the last visitors seen on rosemary plants at the ranch headquarters in August of 2004. We conclude that the introduced exotic European honey bees no longer exist on Santa Cruz Island.

INTRODUCTION

In the 1880s a beekeeper introduced European honey bees (*Apis mellifera*) to Santa Cruz Island and abandoned the project. Those bees then spread over all of Santa Cruz Island but never reached any of the other northern Channel Islands (Wenner and Thorp 1993). Although honey bees have an enviable reputation as a beneficial insect, any introduction of a non-native species can have a devastating effect on native plants and animals (Wenner and Thorp 1994). For example, honey bees may have played a major role in the extinction of the Carolina parakeet, due to bee swarms usurping tree cavities that the parakeets used for nesting (Rosen 2008). Honey bee effects have also been investigated by examining their impact on the nests of both social and solitary bees (Roubik 1983; Sugden and Pyke 1991).

Several reviews exist on the impact of honey bees on natural systems, with a variety of conclusions about this invasive species' overall impact on ecosystems (Sugden et al. 1996; Butz Huryn 1997; Goulson 2003). Our work on Santa Cruz Island began out of concern for the role of honey bees in competing with native pollinators for island plant resources (Wenner and Thorp 1994; Thorp et al. 1994). On various trips to the northern Channel Islands in the 1960s and 1970s, one of us (AMW) had noticed a marked difference in pollinator visitation on flowering plants. For example, manzanita blossoms on Santa Rosa Island had an entire suite of native insects of various families, while those same plant species on Santa Cruz Island had honey bee visitation almost exclusively. Those observations led to the question of how much honey bees had altered the ecological balance on Santa Cruz Island and whether honey bee colony removal might shift the balance in favor of native bees and native plants pollinated by those bees (Wenner and Thorp 1994; Thorp et al. 1994).

During favorable seasons, native species might coexist quite well with honey bees. However, during unfavorable seasons when resources are limited, competition between honey bees and native bees is expected to be more severe (Thorp 1996). For example, during years of drought honey bees have a major competitive advantage in that they have nectar and pollen stores they can rely upon. Many native species, by contrast, have annual life cycles and therefore have no such stores and cannot successfully compete with the introduced honey bees. The native bee species and the plants that rely

on them for pollination then suffer. Consequently, intense scramble and interference competition likely occurs between honey bees and native bees during these drought periods (Wenner and Thorp 1994). We therefore reasoned that removing honey bee colonies from Santa Cruz Island would restore balance between native plants and their pollinators.

The honey bee removal project was initiated in October 1987, when we obtained permission from the island's owner, Dr. Carey Stanton, to begin removal of the exotic honey bee colonies. This effort later became part of The Nature Conservancy's overall goal to remove various European invasive species from the island. In previous publications (Wenner and Thorp 1994; Wenner et al. 2000), we described rationale, goals, scope, and earlier progress in our long-term feral honey bee removal project on Santa Cruz Island in greater detail; below we outline the major points.

Initially we envisioned several benefits from the eradication of honey bees on Santa Cruz Island. The first was to eliminate competition with native bee species on the island. The second was to reduce pollination of weed species, especially those that had co-evolved with honey bees. The third was to facilitate recovery of native plants that rely on pollination by native bee species. The fourth was to provide a field laboratory free of exotic honey bees that would permit unique comparative pollination studies among regions in the United States, as well as elsewhere in the world, including in the native range of honey bees (Eurasia). Later, there was concern that Africanized honey bees, a recent introduction into Santa Barbara County, might colonize Santa Cruz Island. We were not concerned that swarms could cross the Santa Barbara Channel intact on their own, but that drones might be swept across from the mainland by Santa Ana winds. Since Africanized drones aggressively mate with European honey bee queens and their genes are dominant for defensive behavior and absconding, an influx of drones could lead to genetic contamination. This could result in introgression of African honey bee genes into the island population(s), a phenomenon that is difficult to stem in mainland environments (Page and Erickson 1985). Removal of all honey bees would forestall that eventuality and make Santa Cruz Island a safe place for visitors. Although similar attempts failed in mainland venues (Tew et al. 1988), we felt the likelihood of success would increase in an insular island ecosystem. This contribution summarizes the four phases of this honey bee removal project as it evolved through two decades.

METHODS AND RESULTS: FOUR PHASES

First Phase (1988–1993)—Locating and Eliminating Feral Colonies

During the first three years we located colonies by improved bee hunt techniques (Wenner et al. 2000) and mapped those locations. We also gathered background data on floral resource use by honey bees and native bees (e.g., Wenner and Thorp 1994; Thorp et al. 1994, 2000). This early period of the study was designed to develop baseline information on the ecological conditions that characterized Santa Cruz Island before the removal of honey bees.

At the end of the 1990 season we began to eliminate colonies on the eastern half of the island. (See Figure 1 in Wenner and Thorp 1994.) To kill most colonies, we sprayed an aerosol mist of methyl chloroform into the cavities containing them. That mist immediately anesthetized all bees, after which we blocked up all entrances so that bees in that cavity would die. In some cases we had to treat more than once. For colonies that we could not access, we used a remote baiting system employed earlier in the eradication of Africanized honey bee colonies (Williams et al. 1989; Danka et al. 1991).

Following the eradication of colonies, we routinely surveyed the island for the presence of honey bee swarms both in natural (e.g., tree, ground) cavities that had been previously occupied by colonies we had exterminated, and in traps equipped with chemical lures (Schmidt and Thoenes 1990). Swarms are groups of workers with individual queens, which bud off from existing colonies, seek appropriate cavities, and start new colonies. When new swarms were detected, they were exterminated following the methods described above. These efforts to seek out and eradicate new swarms were continued throughout the duration of our project.

By January of 1992, honey bee visitation on plants had declined markedly on the eastern half of the island, while native bee presence increased (see

Wenner and Thorp 1994 for details). By the end of the 1993 season, we had documented the existence of more than 200 colonies and eliminated 153 of them (Wenner et al. 2000). Those totals included swarms caught in traps equipped with chemical lures.

Second Phase (1994–1997)—Biological Control and Colony Demise

From 1994 to 1997 we used biological control to eradicate honey bee colonies. In 1993, heavy rains in January washed out most roads, severely restricting travel around Santa Cruz Island. Fennel thickets had also become impenetrable in many areas following the removal of cattle from the island in 1989 (L. Laughrin, personal communication; A. Wenner, personal observation). Many colonies became inaccessible, rendering our bee hunt techniques (Wenner et al. 1992) ineffective. Therefore, in 1994 we implemented the use of varroa mites (*Varroa destructor*) as an alternative technique for eradicating colonies.

Varroa mites are parasitic on honey bees but apparently not on any other bee or wasp species (Kevan et al. 1991; Wenner et al. 2000). Thus, mites posed no threat to Santa Cruz Island native bees. Previous studies indicated that, even though the European honey bee was not the original host for the mite, it was still very effective in lowering population levels of honey bees (Kraus and Page 1995). These characteristics (high host specificity and the potential for density dependent parasite-host population interactions) suggested an opportunity to use biological control to reduce honey bee levels on Santa Cruz Island. In addition, the use of varroa mites met all 14 requirements for release of biological control agents in Nature Conservancy preserves, as described in a February 15, 1994 memorandum ("Policy on Intentional Release of Non-Indigenous Biocontrol Agents on Preserves Owned or Managed by The Nature Conservancy") forwarded to the authors by Diane Devine of The Nature Conservancy.

In December 1993 and January 1994, we introduced varroa mites to the eastern half of Santa Cruz Island. To introduce mites, we captured 85 honey bees with a net, one at a time, and placed a single mite on each bee. The bees were then released. We continued to routinely monitor the island for the presence of colonies, including new colonies found and new swarms trapped after January 1994 in both natural and artificial cavities. The monitoring involved an average of six visits per year for a total of 25 trips to the island during that four-year period.

During the first two years after varroa mite introduction, the number of swarms observed remained relatively unchanged. However, swarm numbers declined dramatically in 1996, and we did not observe any new swarms in swarm traps thereafter (Fig. 1).

Third Phase (1998–2004)—Monitoring Residual Honey Bee Activity

Despite an absence of demonstrable swarming, we could still find a few individual foraging honey bees at various places and at various times on the island. Accordingly, we traveled about the island several times each year for seven years, documenting the presence of individual foraging honey bees and native bee species (e.g., Thorp et al. 1994, 2000). Nineteen foraging sites were recognized as most likely to have honey bee visitation, due to the existence therein of plants preferred by honey bees. Each year from 1998–2004, we visited a subset of these sites. Timing of site visits followed no set schedule, since visits depended upon the time of year that plants of interest flowered, as noted in Table 1 of Wenner and

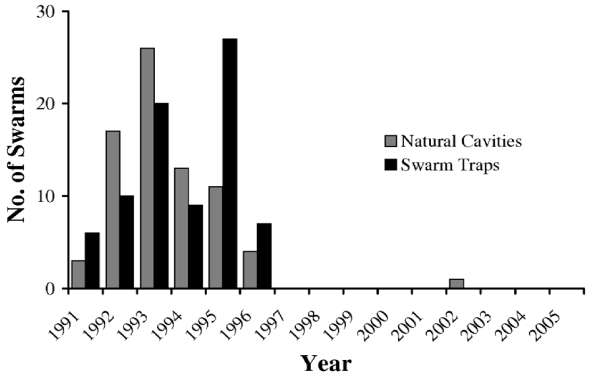

Figure 1. Numbers of new honey bee swarms observed each year on Santa Cruz Island from 1991–2005. Gray bars denote swarms observed in natural cavities that had been previously occupied by colonies we had exterminated. Black bars denote swarms caught in swarm traps.

Thorp (1994). Through time, even though we could still find a few honey bees foraging at a few sites, the numbers present were not sufficient to determine colony location by bee hunt techniques (Wenner et al. 1992).

In addition to visiting foraging sites, we continued to inspect installed swarm traps and insert fresh chemical lures each year in swarm traps located in those regions where honey bees had recently visited target plants. No swarms occupied those swarm traps, though, and the number of sites with honey bee foragers declined steadily year by year.

From our tallies of honey bee foraging distributions and flight lines, it appears that three colonies had survived until 2001. By inference, based on flight line observations, we determined that one colony existed in the lower Laguna Canyon region, one near the Main Ranch complex, and one in the Matanza area to the northwest of the main airstrip.

We located a feral colony at the top of the Matanza grade on August 6, 2002 but found that same colony dead by March 31, 2003. Ten years after a 1993 study in which Barthell et al. (2001) tallied 1,681 foraging honey bees among three plots during one day, we found only three honey bees in just one of the original plots in July of 2003 (Barthell et al. 2004). Another colony must have existed on the island, because a few honey bees were seen on rosemary plants at the Ranch headquarters in July of 2004. By September of that year, though, honey bees were no longer observed foraging at that remaining site.

Fourth Phase (2005–2007)—Confirmation of Honey Bee Absence

For a total of six trips (two each year) during the final three seasons of our project we continued to check swarm traps and inspect 19 foraging sites, although we did not replace lures in the swarm traps. During this period, we did not detect any honey bees. All trips were planned to take advantage of times that target plants would be in optimal bloom. During the final three-year period, Lyndal Laughrin (UC Reserve manager) and David Dewey (TNC Island manager) did not observe honey bees in their extensive travel about the island in the course of their duties (personal communication).

In addition to our consistent revisitations of "hot spots" where honey bees had last been seen, and checking for them foraging at target flowers known to be preferred by honey bees, we also searched additional areas as we traversed the island looking for native bees. Overall, our search efforts were intensified in the last three years, compared to those years when honey bees were present. This search effort at flowers attractive to bees should have

Table 1. Data from 19 target sites monitored for *Apis mellifera* during each of the last eight years.

Season	a) Total # of 19 sites monitored	b) Total # of our visits to those sites	c) Sites that had honey bee foragers	d) Total # of times bees seen	e) # of fresh swarm lures installed	f) # of times trap hives checked	g) # of swarms caught
2000	15	27	9	11	43	122	0
2001	15	24	7	9	27	71	0
2002	11	16	4	5	27	57	0
2003	9	13	2	4	30	41	0
2004	15	24	1	1	28	46	0
2005	10	15	0	0	*	*	0
2006	11	15	0	0	*	*	0
2007	8	13	0	0	*	*	0

* We neither saw nor caught swarms after 1996, so we ceased putting lures in those hives after 2004.

revealed any rare visitation by honey bees, since bees can forage up to more than two miles from their colonies.

SUMMARY OF LAST EIGHT YEARS

In accordance with the limitations described above, during the last eight years of our project we concentrated our observations on the sites where we last saw honey bees foraging (Table 1, column a). Depending on weather and road conditions, as well as time of bloom for target plant species, we had a total of 147 visits to all those sites during the eight-year period (Table 1, column b). The number of sites with foraging bees declined steadily each year during the first five years (Table 1, column c), and the total number of times that we saw bees at any one site also declined at those sites (Table 1, column d). No bees were seen during the final three years at any of the sites we inspected.

During the first five of the last eight years we continued to insert lures into swarm traps (Table 1, column e; 155 lures total) but ceased doing so during the last three years (fourth phase), since we no longer saw any bees foraging at any of the target sites. Neither did we find any swarm traps (both those with new lures and those that had swarm lures inserted earlier) occupied during the 337 times we checked them in this last phase (Table 1, column f). The absence of swarms in column g of Table 1 corresponds with the fact that we saw no swarms after 1996.

DISCUSSION

Since bees are capable of foraging more than two miles from their colonies, and since we found no bees foraging at the "hot spots" we had monitored, we consider it likely, after 20 years of effort, that introduced feral (European) honey bees no longer exist on Santa Cruz Island. While removing the honey bees we eliminated a major competitor for native bee species (Sugden et al. 1996; Butz Huryn 1997; Thomson 2004), gained a more complete survey of native bee species diversity (Thorp et al. 1994, 2000), documented bee species visitation on both native and exotic plants (Wenner and Thorp 1994; Thorp et al. 1994, 2000; Barthell et al. 2000), studied native bee and honey bee pollination of native and exotic plants (Barthell et al. 2000, 2001, 2005), contributed to biogeographical understanding by documenting the composition of the bee communities on islands compared to somewhat equivalent mainland areas (Thorp et al. 1994, 2000), enhanced our knowledge of honey bee foraging behavior and colony distribution (Wenner et al. 1992; Wenner and Thorp 1994; Thorp et al. 1994, 2000), reduced or eliminated the threat of island colonization by Africanized honey bees (Wenner and Thorp 1994), tested the effectiveness of varroa mites as a biological control against honey bees (Wenner et al. 2000; Wenner and Thorp 2002), and documented the rate at which varroa mites could eliminate honey bee colonies in a region (Wenner and Thorp 2002).

In retrospect, our success is due to several factors. First, Santa Cruz Island is a closed ecosystem, with the long distance over water providing a barrier to unaided invasion by honey bees. Second, there was little opportunity for honey bees to evolve resistance to the varroa mites, since honey bees on the island had essentially no genetic variability (Wenner and Thorp 1993). The relatively short duration of our project also permitted no time for mite and honey bee coevolution, and the European honey bee is not the original host of the mite. Third, varroa mites can survive only in honey bee colonies (warm conditions, with live bees and/or brood year round), making them a good biological control agent that is unlikely to adversely affect native bee species.

We eliminated a known total of 300 colonies by the use of physical and biological controls, while parasitic mites (our biological control agent) likely eliminated a number of other honey bee colonies that we had not previously detected on Santa Cruz Island. Our accomplishment may be a rare case, where an introduced exotic biological control agent has apparently completely eliminated another introduced exotic species, although cases of virtually complete "control" have been recorded, including the case of the cottony cushion scale, *Icerya purchasi* Maskell, in southern California citrus orchards (Caltagirone and Doutt 1989). Santa Cruz Island itself is the venue of the often cited case of the cochineal insect *Dactylopius opuntiae* (Cockerell) reducing cactus (*Opuntia* spp.) populations (Goeden and Ricker 1981). However,

even that major biological control (cochineal) success had less dramatic results than the case of varroa impacting honey bee colonies on the island. Indeed, one might consider this current case as one of "biological eradication" rather than one of classical biological control *per se*. The use of varroa mites also differs from classical biological control because the European honey bee was not the coevolved host of the control agent: rather, the Asian honey bee *Apis cerana* Fabr. served in that role. In addition, we did not travel to the native range of the host to collect the control agent, as is the practice in classical biological control programs.

Aside from elimination of an exotic species, our adverse impact on the island ecology has been minimal. Extensive observations of native bee abundance and diversity both before and after varroa introduction indicate that no other species of Hymenoptera on Santa Cruz Island have been negatively impacted (Thorp et al. 1994, 2000). Also, varroa mites are known to be very specific to the non-native honey bee genus *Apis* for their reproduction—although those mites can be dispersed by non-*Apis* species (Kevan et al. 1991). The only potential drawback to our operation may be the monitoring materials we used during the last 20 years. At the peak of our study, we had 134 swarm traps installed about the island, with an additional 15 installed during the last several years. These asphalt/paper pulp hives, formed in a flowerpot mold and fitted with a lid (Schmidt and Thoenes 1990), were very durable when first installed. Over time, however, the asphalt vaporizes. We replaced traps whenever they became too fragile to hold the weight of a bee colony or removed them when bees no longer foraged in given areas. Also, since we caught no swarms anywhere on the island after 1996, the reduced number of swarm traps mattered little.

During our October 2006 visit to the island, we removed most of the remainder of the intact traps and brought them back to the mainland. Exceptions were as follows: 17 swarm traps were missing from their original installation sites, perhaps blown down by wind and moved about by pigs; five swarm traps had become so thoroughly engulfed by the vegetation around them that they could not be removed; we abandoned 14 swarm traps located in brush too dense for retrieval or in terrain too dangerous for safe retrieval; and one swarm trap had become occupied by a yellow jacket colony during the 2006 season, and was not removed. In time, any remaining swarm traps will reach the ground, become wet with rain, and disintegrate.

Ongoing Studies

Monitoring of native bees on Santa Cruz Island continues. As of April 2007, the number of bee species that have been found on Santa Cruz Island stands at 121 species in 5 families and 35 genera (R. Thorp, unpublished data). This increase of seven species since our last report of 114 (Thorp et al. 2000) is mainly due to refinements in identifications of previous specimens. At least one of these, *Megachile apicalis* Spinola, is a non-native species that we have recently detected in its native Eurasian habitats in association with the invasive weed yellow star-thistle (J. Barthell, unpublished data). This species continues to spread across the island in correlation with the spread of yellow star-thistle (Thorp et al. 2000).

Honey bees have not been detected by any sampling method since July 2004 and have not been major players in the island bee fauna since 1996 (e.g., no more swarms caught in swarm traps), when the introduced varroa mites began to rapidly decimate the European honey bee populations (Wenner and Thorp 2002). However, dramatic increases in populations of native bees have not yet been observed, perhaps for several reasons (Thorp 1996). Any changes are likely to be small and subtle, since most native bees are K-strategists (relative to honey bees) that emphasize considerable maternal investment in provisioning for a few young and often have a single generation per year, rather than r-strategists that produce large numbers of eggs and are multivoltine. Indeed, other environmental changes may have more noticeable impacts on native bee population fluctuations (e.g., drought, excess rains, displacement of native flora by invasive weeds such as fennel and yellow star-thistle, diseases, and other natural enemies) than the effects of sporadic competition for limited food resources.

Although our understanding of resource competition among honey bees and solitary bees on Santa Cruz Island is still in its infancy, a few observations deserve consideration. The presence of the honey bee has been demonstrated to increase the reproductive capacity of highly invasive plants,

including yellow star-thistle on Santa Cruz Island (Barthell et al. 2000, 2001). We also know that this same plant species is a strong competitor with other plant species in the California grasslands and has been expanding its range at a remarkable rate during the last several decades (Pitcairn et al. 2006). Although many native bee species also utilize yellow star-thistle as a source of nectar and/or pollen (Thorp et al. 1994), the loss of native plant habitat is due, at least in part, to honey bee effects; oligolectic bee species, surviving on less common native plant species that compete with yellow star-thistle, may therefore be at risk. Furthermore, when given a choice, we have found that many native species will leave their primary native host plants (e.g., gumplant or *Grindelia camporum* E. Greene) to visit yellow star-thistle. There may be many other cases of host plant overlap between native bees and honey bees (see Thorp et al. 1994, 2000).

One possible increase in population abundance of a native bee that may be related to decline in honey bee populations seems evident. *Halictus farinosus* has been more apparent in recent years (R. Thorp, unpublished data). This sweat bee is a solitary ground nesting species with females slightly smaller than honey bee workers and is broadly polylectic in its choice of pollen plants. Due to its similar size and wide floral resource use, this species overlaps greatly with honey bees for food and may be showing release from competition for floral resources. Indeed, this species was recorded for the first time on yellow star-thistle only after the decline of honey bees (Barthell et al. 2004). As an annual species it would never have the same impact on island pollination as honey bees.

Recently, we have begun comparative investigations between Santa Cruz Island and the island of Lesvos in Greece to investigate the roles of mutualists (bees) and competitors (plants) that influence the success of yellow star-thistle in the western USA, including Santa Cruz Island. Lesvos is the largest of the Northeast Aegean Islands off the western coast of Turkey; both honey bees and yellow star-thistle are native to this location. Like Santa Cruz Island, Lesvos has an increasingly well-characterized bee pollinator community (Petanidou and Lamborn 2005). Our efforts have already begun to characterize the native pollinator guild of yellow star-thistle. We hope our findings will shed light on competitive effects among pollinators and plants as described above, including the role that nectar plays in the success of invasive plant species like yellow star-thistle.

It should be noted that yellow star-thistle requires outcrossing by pollinators to reproduce (Sun and Ritland 1997). Thus, with the honey bees now gone from Santa Cruz Island, the exotic yellow star-thistle (with its primary exotic pollinator) could now decline in abundance on Santa Cruz Island. The seed bank of that species should become depleted, a process that could take years or even decades to complete (Joley et al. 1992; Callihan et al. 1993). This issue is further complicated by the fact that at least two phytophagus fruit fly species have also reached the island since 1993 (J. Barthell, unpublished data), and could further negatively impact yellow star-thistle abundance. Regardless, we predict that several such manifestations of the extinction of the non-native honey bee in the future will result in a return to a more natural ecological balance on Santa Cruz Island.

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ERADICATION OF BLACK RATS FROM FARALLÓN DE SAN IGNACIO AND SAN PEDRO MÁRTIR ISLANDS, GULF OF CALIFORNIA, MEXICO

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Abstract—In the Gulf of California, Mexico, several islands have been severely impacted by introduced rats (*Rattus* spp.). A rat eradication project for Farallón de San Ignacio and San Pedro Mártir islands, both globally important seabird colonies, unfolded from planning and baseline studies in 2005 to implementation in 2007. Rats were eradicated via aerial helicopter broadcast of bait, the only method used to date to eradicate rats from large and topographically complex islands. A special aerial bucket developed in New Zealand (Helicopters Otago) was used for the helicopter dispersion of CI-25, a special formulation of Brodifacoum in the form of pellets, provided by Bell Labs. Eradication occurred in September 2007 on Farallón de San Ignacio and in October–November 2007 on San Pedro Mártir. Initial post-eradication monitoring resulted in no sign of rats. There were no losses of native fauna at a population level. Post-eradication monitoring will continue throughout 2008–2009 to confirm both rat absence and ecosystem recovery. Interinstitutional cooperation was essential in achieving complex permitting, logistics, and financial challenges. This project represents the first project of aerial broadcast rat eradication in Latin America.

INTRODUCTION

Introduced vertebrates are known to be a major cause of extinctions and other dramatic changes on islands (Mack et al. 2000; Blackburn et al. 2004; Reaser et al. 2007). In particular, the impact of rats (*Rattus* spp.) on native island plants, invertebrates, and vertebrates has been well documented (Whitaker 1973; Campbell 1991; Cree et al. 1992; Navarrete and Castilla 1993; Lee and Yoo 2002; Towns et al. 2006). Rats are present on about 85% of the world's island chains (Atkinson 1985) and have caused 40%–60% of all bird and reptile extinctions since 1600 (Groombridge 1992).

Two islands that have been impacted by rat introductions are Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM) islands in the Gulf of California, México (Fig. 1). Both islands support seabird colonies of national and international importance (Tershy and Breese 1997; González

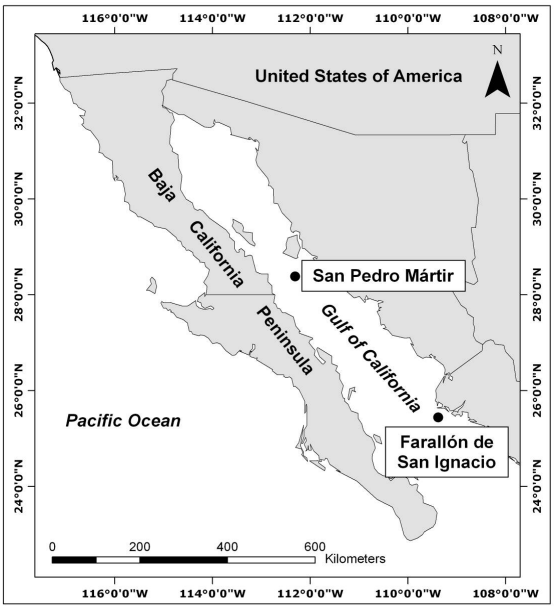

Figure 1. Locations of Farallón de San Ignacio and San Pedro Mártir islands, México.

Bernal et al. 2002), are part of a World Heritage Site (UNESCO), and are legally protected by Mexican law as Natural Protected Areas. Black rats (*Rattus rattus*) are thought to have been accidentally introduced to both islands during guano mining activity in the early 1900s (Tershy et al. 1997). Precise information about local impacts of introduced rats on these islands is scarce (Velarde and Anderson 1994). However, rats are known to have impacted island populations through predation on seabird eggs and chicks on both islands, and fruits and flowers of the cardón (giant cactus; *Pachycereus pringlei*) on SPM (Tershy et al. 1997; A. Samaniego, personal observation). Additionally, the absence of nocturnal seabirds despite suitable habitat on both islands, limited distribution of fishing bats (*Myotis vivesi*) on SPM, and extremely low abundance of the gecko (*Phyllodactylus homolepidurus*) on FSI, are all considered probable consequences of rat predation (Tershy et al. 1997; González Bernal et al. 2002; Frick and Heady 2007; Peralta-Garcia et al. 2007).

To promote the natural restoration of FSI and SPM islands, a rat eradication plan was developed in 2005. The project was headed by the Mexican private organization Grupo de Ecología y Conservación de Islas (GECI), in collaboration with Mexican government agencies SEMAR, SEGOB, CONANP, and SEMARNAT. GECI´s sister organizations in the United States (Island Conservation) and Canada (IC Canada), as well as Prescott College in Bahía Kino, were the main collaborators in fundraising, planning, and local support, respectively. Prior to 2006, four rat eradications had been attempted on Mexican islands by putting out stations containing poison baits (Tershy et al. 2002). Three of these eradications (Rasa, San Jorge, and San Roque islands) were successful (Tershy et al. 2002), and one of them (Isabel Island) failed (Rodríguez et al. 2006). All three islands with successful eradications were less than 50 ha in area, whereas Isabel Island was 82 ha, suggesting that the bait station technique may not effectively eradicate rats on larger islands where not all rats can access the bait stations. Because FSI and SPM islands are topographically complex and SPM is large (267 ha), we opted to use a helicopter to disperse rodenticide broadly across each island. Although used effectively elsewhere (Howald et al. 2007), this was the first time that this aerial procedure was applied in Latin America. The rat eradication project therefore included a 2-year pre-eradication phase in which we acquired baseline population data on rats, and conducted studies to test whether rodenticide pellets were likely to be consumed by native vertebrates. Here we present the results of these preliminary studies, describe the aerial application of rodenticide to each island, and report initial results of post-application monitoring.

METHODS

Site Description

Farallón de San Ignacio (25° 26’ 11.5” N, 109° 22’ 45.5” W) is a small island (17 ha) located 27 km off the coast of Sinaloa state, México (Fig. 1). It is a tall rock with vertical walls and a flat top at 137 m.a.s.l. (Fig. 2a). Vegetation is completely non-existent. The island is an important seabird nesting site. Blue-footed booby (*Sula nebouxii*), brown booby (*S. leucogaster brewsteri*), red-billed tropicbird (*Phaeton aethereus*), and Heermann´s

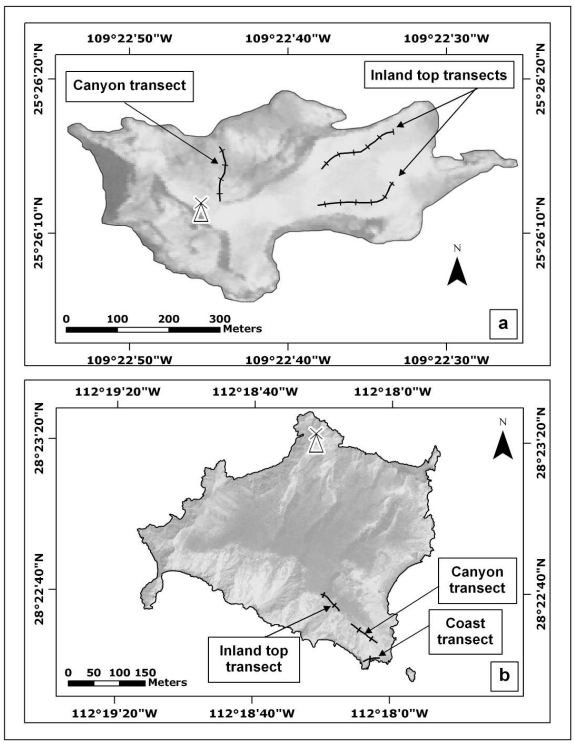

Figure 2. Permanent trapping transects on (a) Farallón de San Ignacio and (b) San Pedro Mártir islands.

gull (*Larus heermanni*) are the most abundant species (González-Bernal et al. 2002). Besides seabirds, the other native vertebrates are three species of lizards (*Aspidoscelis tigris*, *Urosaurus ornatus*, and *Phyllodactylus homolepidurus*; González Bernal et al. 2001a; González Bernal et al. 2001b; Peralta-García et al. 2007) and the California sea lion (*Zalophus californianus*). No native terrestrial mammals occur on the island (CONANP 2000; Case et al. 2002). The only introduced mammal was the black rat *R. rattus* (González-Bernal et al. 2002).

Located 60 km off the coast of Sonora state, México, San Pedro Mártir (28° 23' 0.0" N, 112° 18' 30.0" W) is the most isolated island in the Gulf of California (Fig. 1). The island is 267 ha with a maximum altitude of 305 m.a.s.l., and is dominated by mountainous cliffs (Fig. 2b). It hosts 27 species of plants (cardón forest being the predominant vegetation), 53 of terrestrial birds, 36 of seabirds (8 nesting), 4 of reptiles, and 1 of pinnipeds (Tershy and Breese 1997; Grismer 2002; CONANP 2007). SPM supports some of the biggest populations in the world of blue-footed boobies (*S. nebouxii*), brown boobies (*S. leucogaster brewsteri*), and red-billed tropicbirds (*P. aethereus*). No native terrestrial mammals occur on the island (Case et al. 2002; CONANP 2007). The only introduced mammal was the black rat *R. rattus* (CONANP 2007).

Pre-Eradication Rat Monitoring

To collect baseline data on rat populations prior to application of rodenticide, we established three permanent transects on each of the two islands in May 2005. On SPM the three transects represented the three main habitat types: coast, canyon and inland top (Fig. 2b). Because it was logistically unfeasible to trap along the coast on FSI, we established two transects on the inland top and one transect along a steep canyon (Fig. 2a). Each transect included 15 trapping points at intervals of 20 m. At each point we set 3 devices separated by 2 m: one Tomahawk trap (Tomahawk Live Trap Co, Tomahawk, WI), one Sherman trap (H.B. Sherman trap, Tallahassee, FL), and one indicator block (peanut-flavored wax chew block). Especially for islands without native rodents, indicator blocks are a very useful, inexpensive and practical tool for detecting rodent presence. Traps and blocks were set and checked for three consecutive days at each trapping session. All traps were opened before sunset, baited with a mix of oats and peanut butter, and checked in the morning. Indicator blocks were set the first afternoon, checked every morning and replaced if they showed any mark. Data recorded included island, date, transect, trapping point, trap type, species captured, and marks on the block (none, rodent bites, and other marks).

Systematic trapping combined with indicator blocks was conducted every three months on both islands from fall 2005 to summer 2007, except fall 2006 for FSI and winter 2006 for both islands. This resulted in one trapping period in fall (2005), one in winter (2005), two in spring (2006, 2007), and two in summer (2006, 2007) on FSI; and two trapping periods in fall (2005, 2006), one in winter (2005), two in spring (2006, 2007), and two in summer (2006, 2007) on SPM. On FSI total capture effort represented 1319 trap-nights and 475 block-nights. On SPM total capture effort represented 1513 trap-nights and 435 block-nights. Percent capture success for each trapping period was calculated according to the number of individuals captured per trap-nights (Tomahawk and Sherman traps combined) given habitat type and trapping date. All captured individuals (100% *R. rattus*) were humanely sacrificed with the anesthetic Pentobarbital sodium (Aranda Labs, Querétaro, Querétaro, México).

Choice of Rodenticide and Potential Impacts on Native Fauna

Bait used was the rodenticide CI-25, developed by Bell Labs (Madison, WI) especially for ecological restoration projects, and proven successful on Anacapa Island in the Channel Islands in 2001 and 2002 (Howald et al. 2005). CI-25 are green, unwaxed, compressed grain, 2 gm pellets containing 25 ppm brodifacoum, which is a second generation anticoagulant. Prior to rat eradication and in order to assess if CI-25 pellets were attractive to island fauna, we conducted palatability experiments of placebo bait on reptiles, seabirds, and fishes (Table 1) on April 3–7, 2006 on FSI and on April 11–16, 2006 on SPM. Placebo bait was also manufactured by Bell Labs and had the same characteristic of the toxic bait except for the rodenticide brodifacoum.

We tested all reptile species whose diet could include grain-type components, and excluded

Table 1 . Species, methods, and reaction of vertebrates exposed to placebo bait pellets of CI-25 (brodifacoum) on Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM) islands.

Species	Family	Island	Method of exposure	Reaction
Fishes				
Prionurus punctatus	Acanthuridae	FSI	Natural conditions	No consumption
Balistes polylepis	Balistidae	SPM	Natural conditions	No consumption
Ophioblennius steindachneri	Blenniidae	FSI, SPM	Natural conditions	Inspection, no consumption
Cirrhitus rivulatus	Cirrhitidae	FSI	Natural conditions	No consumption
Diodon holocanthus	Diodontidae	FSI	Natural conditions	No consumption
Haemulon sexfasciatum	Haemulidae	FSI, SPM	Natural conditions	No consumption
Girella simplicidens	Kiphosidae	SPM	Natural conditions	No consumption
Bodianus diplotaenia	Labridae	SPM	Natural conditions	No consumption
Semicossyphus pulcher	Labridae	SPM	Natural conditions	No consumption
Thalassoma lucasanum	Labridae	FSI, SPM	Natural conditions	No consumption
Lutjanus argentiventris	Lutjanidae	SPM	Natural conditions	No consumption
Lutjanus novemfasciatus	Lutjanidae	SPM	Natural conditions	No consumption
Holacanthus passer	Pomacanthidae	FSI, SPM	Natural conditions	No consumption
Microspathodon dorsalis	Pomacanthidae	SPM	Natural conditions	No consumption
Stegastes acapulcoensis	Pomacentridae	FSI	Natural conditions	No consumption
Stegastes flavilatus	Pomacentridae	FSI	Natural conditions	No consumption
Abudefduf troschelii	Pomacentridae	FSI, SPM	Natural conditions	No consumption
Chromis atrilobata	Pomacentridae	FSI, SPM	Natural conditions	No consumption
Cephalopholis panamensis	Serranidae	SPM	Natural conditions	No consumption
Epinephelus labriformis	Serranidae	FSI	Natural conditions	No consumption
Mycteroperca rosacea	Serranidae	SPM	Natural conditions	No consumption
Paranthias colonus	Serranidae	FSI, SPM	Natural conditions	No consumption
Axoclinus carminalis	Tripterygiidae	SPM	Natural conditions	No consumption
Reptiles				
Urosaurus ornatus	Phrynosomatidae	FSI	Natural conditions	Inspection, no consumption
Uta palmeri	Phrynosomatidae	SPM	Natural conditions and captivity	Inspection, no consumption
Aspidoscelis tigris	Teiidae	FSI	Natural conditions and captivity	Inspection, no consumption
Aspidoscelis martyris	Teiidae	SPM	Natural conditions	Inspection, no consumption

Table 1 (continued). Species, methods, and reaction of vertebrates exposed to placebo bait pellets of CI-25 (brodifacoum) on Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM) islands.

Species	Family	Island	Method of exposure	Reaction
Birds				
Larus heermanni	Laridae	FSI, SPM	Natural conditions	No consumption
Sula leucogaster brewsteri	Sulidae	FSI, SPM	Natural conditions	No consumption
Sula nebouxii	Sulidae	FSI, SPM	Natural conditions	No consumption

species with strictly carnivorous diets (e.g., *Phyllodactylus homolepidurus, Lampropeltis getula nigritus,* and *Crotalus atrox*). Twenty adult lizards (10 *Aspidoscelis tigris* on FSI and 10 *Uta palmeri* on SPM) were individually kept in captivity for 5 days in wired cages (90 x 45 x 45 cm) on their respective island. Each individual was offered a 2.0 gm pellet, which was subsequently weighed and checked for bite signs every 24 hrs. Along with the experiment, we made *in situ* observations on adult and juvenile individuals of four species of lizards (*A. tigris* and *Urosaurus ornatus* on FSI; *Uta palmeri* and *A. martyris* on SPM). Between 10:00 and 11:00 a.m., we spread out 10 pieces of placebo bait inside plots of approximately 10 m^2 in different microhabitats (shoreline, canyon, inland top). In each trial (n = 15 per island), we observed the reaction of each species for 15–30 minutes. Reactions to pellets were categorized as a) no consumption (pellets ignored), b) inspection but not consumption, or c) consumption.

For birds we conducted *in situ* observations in order to include the most species possible. Because terrestrial birds are present at very low abundance, they were never present during our observations. Despite the fact that most of the nesting seabirds are piscivorous, we were interested in the reaction of ground nesting seabirds to bait pellets. Observations were conducted during morning hours on areas with abundant individuals (> 50) for five consecutive days on each island. In each trial (n = 15 per island), we placed 10 pieces of placebo inside plots of approximately 50 m^2. Reaction of each species was recorded during 30–60 minutes. Reactions to pellets were categorized as a) no consumption (pellets ignored), b) inspection but not consumption, or c) consumption.

Since the probability of spreading bait beyond 10 m offshore of the islands was minimal, we focused our fish observations on waters immediately adjacent to the islands. Seven underwater observation sessions were conducted (four on FSI and three on SPM). Each session took place in a different day, during the afternoon, and lasted for an hour. At each session one person with free diving equipment remained 3–5 m from shore and made observations along the water column up to 15 m deep. In each event, 10 pieces of placebo were thrown to the ocean. Species present and reaction to pellets were recorded. Reactions were categorized as a) no consumption (pellets ignored), b) inspection but not consumption, or c) consumption.

Bait Application

Because of the size, steepness, and ruggedness of FSI and SPM islands, the most feasible option for achieving eradication was to disperse bait pellets using an aerial drop technique, developed in New Zealand (Towns and Broome 2003) and used previously in several countries (Howald et al. 2007). The bait was broadcast from a helicopter using a stainless steel spreader bucket built in New Zealand (Helicopters Otago, Mosgiel, New Zealand). The helicopter (Bell 206 from Aspen Helicopters, Oxnard, CA) was equipped with a differential GPS to obtain geographic data with high accuracy. A GIS was built to confirm that distribution and application rate within each topographic category area were correct according to planning. On both islands bait was applied to 100% of the island surface. Cliff and canyon areas were treated twice during each drop to allow for the increased planar area that had to be covered. When applying bait to the cliffs, a lateral deflector was adapted on the bucket to narrow the angle of bait dispersion and

minimize the amount of bait spread into the ocean. Because the intertidal zone represents prime habitat for rats, a detailed hand broadcast was conducted by small boat (along shoreline) and by helicopter (above islets) the next day after each aerial drop to ensure adequate bait application. To track the aerial work and map rodenticide densities in the ground, we used a 60 cm per pixel resolution Quickbird satellite image (© 2006 Digital Globe Inc.) of SPM, and an aerial photo of FSI.

Climate and reproductive cycles of both introduced and native species are the main factors to be taken into account for timing rat eradications (Howald et al. 2005). In this case, timing of bait application was determined by weather (dry season), seabird and sea lion activity (non-reproductive season), and rat population activity (low breeding rate). The eradication operation on FSI was carried out on September 27, 2007, with the helicopter operating out of the Mexican Navy base in Topolobampo, Sinaloa, 29 km from the island. A total of 567.5 kg of bait was broadcast by helicopter using a single aerial bait drop and 90 kg of bait was broadcast by hand along shoreline and islets. On average, bait was applied at a rate of 24.4 kg/ha (Fig. 3a). The operation on SPM included two bait drops. The operation base for the first drop was the Mexican Navy MV Sonora (PO152), an oceanic patrol vessel from the Mexican Navy provided for the project that anchored in front of the island. The drop occurred on October 31, 2007. The second drop was based on the island and occurred nine days later on November 9, 2007, with logistics support from the MV Guadalupe, also from the Mexican Navy. Average bait density broadcast was 17.6 kg/ha (Fig. 3b). A total of 5,902.5 kg of bait was broadcast by helicopter and 440 kg by hand along shoreline and islets.

Underwater monitoring was conducted 24 hours after each aerial broadcast, in both the intertidal and sublittoral zones of the two islands. The dive focused primarily in assessing the invertebrate and fish communities, as well as the sea lion colonies. Underwater photographs were taken.

Confirmation Monitoring

The first eradication confirmation monitoring on FSI was carried out seven weeks after the drop, on November 14–17, 2007. 105 Tomahawk traps and 260 indicator blocks were set along permanent

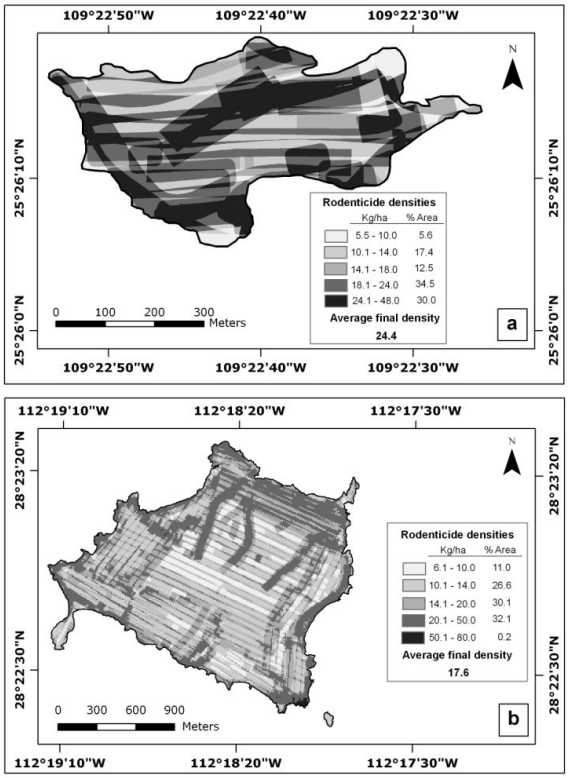

Figure 3. Bait density after (a) a single broadcast on Farallón de San Ignacio Island and (b) a double broadcast on San Pedro Mártir Island, in fall 2007.

transects and around areas with known high rat activity, for three consecutive nights. Capture effort represented 315 trap-nights and 780 block-nights. All accessible areas were walked searching for carcasses (of rats or native species) and signs of rats.

On SPM, it was not possible to return weeks after the drop due to financial and logistic limitations. Therefore, the initial confirmation was based on monitoring of radio-collared rats. Twelve adult females (average weight = 156.2 gm ± 30.3) and 13 adult males (average weight = 178.2 gm ± 36.5) were captured in different habitat types and radio-collared 12 days before the first drop. All were released at the capture spot and monitored every night. Based on telemetry indications, 24 individuals were active the day of the first drop. One collar may have become damaged because the signal was lost days before the drop. After the drop, individuals inactive for 2–3 days were assumed to be dead and were subsequently recovered from underground burrows. Date of death was estimated based on carcass condition. All recovered individuals were dissected to confirm cause of

death. Nine days after the first drop, we walked five 500 m transects spread over island, looking for carcasses (of rats or native species) and signs of rats. Thirty-two circular monitoring plots of 3 m radius (28.27 m^2), chosen randomly around the island before the drops, were searched in greater detail to maximize the probability of finding small animals.

RESULTS

Rat Monitoring

Prior to the application of rodenticide, capture success varied between islands, seasons, and habitat types (Fig. 4). On FSI, 238 individuals of *R. rattus* were caught from a total capture effort of 1319 trap-nights (18.0% capture success). The highest mean seasonal capture rate was in summer ($\bar{x}$ =29.8%; Fig. 4a), and the highest mean capture rate among habitat types was in inland top ($\bar{x}$ =18.1%; Fig. 4a). 38.1% of all indicator blocks were chewed by rats. On SPM, 252 individuals of *R. rattus* were caught from a total capture effort of 1513 trap-nights (16.7% capture success). The highest seasonal mean capture rate was in summer ($\bar{x}$ =32.1%; Fig. 4b). Of the habitat types, the highest mean capture rate was in canyon ($\bar{x}$ =25.1%; Fig. 4b). Rats chewed 21.1% of all indicator blocks.

On FSI, preliminary trapping following application of bait yielded no captures of rats, and there was no evidence of rat chewing on indicator blocks. No rat carcasses were found during searching walks. On SPM, 19 of 24 radio-collared rats were recovered dead, along with one dropped collar. Of the remaining four collared rats, three were located in inaccessible locations (vertical cliffs and under massive rocks); and one, including the active collar, was devoured by a rattlesnake. All recovered rats died underground between 3 and 7 days after the first drop. Dissection of 21 individuals (19 collared plus 2 non-collared found while digging for the first ones) confirmed poisoning as the cause of death in 100% of the rats. Furthermore, stomach content in most individuals was 90% bait. During searching walks and inspections of verification plots, we found two fresh rat carcasses.

Impacts on Native Fauna

Table 1 shows a summary of palatability experiments. None of the reptiles in captivity consumed bait; all pellets weighed the same at the end of the experiment as at the beginning, and none showed bites. As for the *in situ* observations, the only reaction recorded for all species and islands was "inspection but not consumption." Seabird species present during the observations were *S. nebouxii, S. leucogaster brewsteri*, and *Larus heermanni*. The only reaction recorded for all species and islands was "not consumption." On FSI 13 fish species of 9 families (Table 1) were recorded during the observations, whereas on SPM 17 species of 10 families (Table 1) were recorded. Of a total of 23 fish species observed, 22 did not consume pellets. For the last species (*Ophioblennius steindachneri*), one individual out of a dozen observed ate one piece, but spit it out. The same species was observed on SPM, but was not observed to consume bait pellets.

Twenty-four hours following application of rodenticide, underwater monitoring at both islands

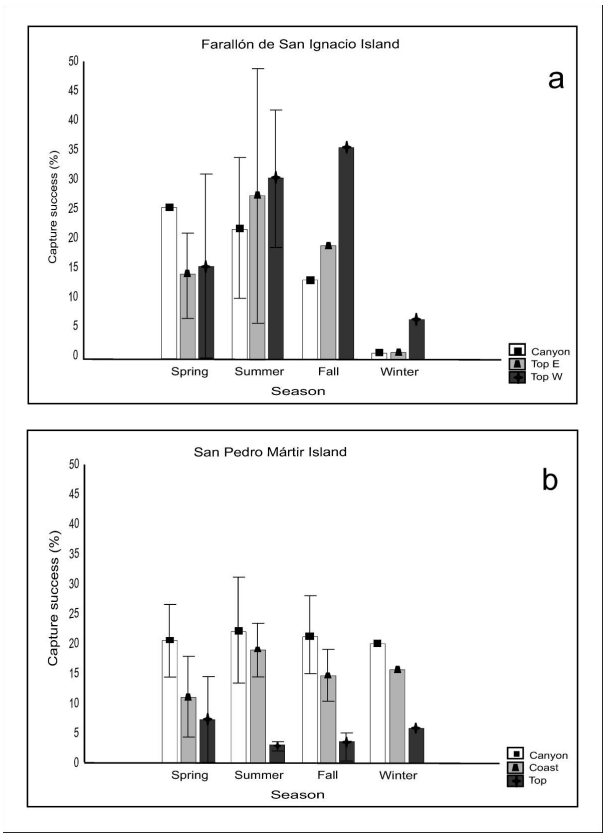

Figure 4. Percentage of capture success of pre-eradication rat trapping per habitat type, on (a) Farallón de San Ignacio Island and (b) San Pedro Mártir Island, from 2005–2007. Heights of bars indicate means, and error bars indicate maximum and minimum values.

found no traces of pellets on either the sea floor or in tide pools. Five species of invertebrates: red rock crabs (*Grapsus grapsus*), barnacles (*Balanus spp.*), sea urchins (*Echinometra vanbrunti*), and sea stars (*Pharia pyramidata* and *Phataria unifascialis*); 13 fish species of 9 families (Table 1), and sea lions (*Z. californianus*), were recorded in normal conditions in terms of behavior and external aspect.

Seven weeks after the drop, advanced degradation of leftover bait was evident. On the inland´s top of FSI, 11 small terrestrial birds (8 *Passer domesticus*, 2 *Columbina passerine*, and 1 *Carpodacus mexicanus*) were found dead, possibly by rodenticide ingestion. Carcasses were too dry to dissect and confirm cause of death. Blue-footed boobies, brown boobies, and red-billed tropicbirds had laid the first eggs of the season and all were intact, without rat chews. During searching walks and inspections of verification plots on SPM, we found seven fresh bird carcasses: six yellow-footed gulls (*Larus livens*) and one common raven (*Corvus corax*), which may have died from poisoning. All lizards, snakes, and other birds observed during the searching walks looked in normal condition in terms of behavior and external aspect.

DISCUSSION AND CONCLUSIONS

Two years of planning, testing, and monitoring were necessary to obtain the basic information for development of a detailed strategy for eradicating rats on FSI and SPM islands, and to comply with complex permitting requirements. Baseline data acquired from pre-eradication monitoring facilitates the confirmation of both eradications, as well as the planning of other eradication and conservation actions in the region. As expected, rats on SPM died between days three to seven after the first bait drop. Initial results indicate that the rat eradications on both FSI and SPM islands were successful.

We believe that application of the rodenticide CI-25 to FSI and SPM islands resulted in minimal adverse effects to island fauna. Results of palatability experiments with the abundant native species suggest that bait pellets intended for rats are not likely to be attractive to many native fish, reptiles, or seabirds. Of the 29 vertebrate species exposed to the placebo bait, 96.5% were not interested in it, and the few that were attracted (three reptiles, one fish) did not consume even one pellet. Nevertheless, because of their migratory habits, behavior, and potential susceptibility, birds need special attention and more studies. Overall, the loss of native fauna after the broadcast was insignificant at a population level. However, some mortalities were observed during monitoring that may have resulted from rodenticide poisoning: 11 terrestrial birds (3 species of passeriforms) on FSI as well as 7 seabirds (6 yellow-footed gulls and 1 common raven) were found dead. None of these species are abundant on the islands and were not present during our palatability tests. Since these passeriform species are granivorous, and seagulls and ravens are generalists, primary poisoning may have been the cause. Seagulls and ravens are also scavengers and therefore are exposed to secondary poisoning as well. At the same time, since rats die underground they are not expected to be available for scavengers, and insects are not susceptible to anticoagulants. Therefore, impacts via secondary poisoning are expected to be minimal. However, a detailed and specific plan for each case, containing mitigation actions for both marine and terrestrial ecosystems, is obligatory. For example, during the black rat eradication in 2001–2002 on Anacapa Island, endemic mice were taken into captivity and raptors were temporarily maintained at a prudent distance from the island (Howald et al. 2005).

Following application, no traces of pellets or signs of negative environmental impact were found at the intertidal and sublittoral zone of FSI and SPM islands, and it appears that the deflector was successful in minimizing the number of bait pellets broadcast into the ocean. Consistent with other aerial rat eradications (Howald et al. 2005; Hoare and Hare 2006), marine invertebrate and fish communities did not appear to be negatively affected by the low amount of bait that fell into the water. No signs of poison-caused death were found in marine species. Helicopter disturbance to fauna was inconsequential, as the operation lasted only a few days and did not occur during the reproductive season for seabirds or pinnipeds.

Conventionally, formal protocols on rodent eradications establish that success can be declared after two years of the eradication, since rodents at low densities are difficult to detect (Howald et al. 2007). Post-eradication monitoring on these islands will continue seasonally, every three months. Once

the eradication is fully confirmed in fall 2009, the long-term monitoring will focus in those habitats and seasons where rats used to be more abundant. We expect post-eradication monitoring throughout 2009 to confirm both rat absence and ecosystem recovery. This project represents the first aerial broadcast rat eradication in Latin America and the second in North America.

Interinstitutional cooperation has been key to achieving the complex permitting, logistic, and financial challenges. The Mexican Navy, well above and beyond its mandate, has been actively engaged during the last years in island conservation projects (Aguirre-Muñoz et al. 2008). In this case, the Navy supported the helicopter operation by providing a modern vessel with helicopter platform and hangar as an in-kind donation. Also, the project got the backing from the Navy's facilities and the personnel on the mainland. The Ministries of the Interior (Gobernación) and Environment (SEMARNAT) have moved from a traditional regulatory and supervising role to a more proactive one (Aguirre-Muñoz et al. 2008). The teams in the field had the participation of technical personnel from the Protected Areas Commission (CONANP); for the CI-25 special bait importation, the CONANP's head, Ernesto Enkerlin personally assumed responsibility in front of customs and health authorities. This intense teamwork between a private organization and federal agencies is the result of trust and confidence gained during several years, honored commitments, and shared successful results. Because of the logistical complexities of working on islands, and once Mexican islands are federal territories, for future similar projects in Mexico the same commitment and support of Mexican government agencies is a must.

Based on what we can define as a focused collaboration approach, the "winning strategy" for eradicating 43 introduced mammal populations on 28 Mexican islands during the last decade integrates 3 main elements: (1) a persistent and capable private organization leading the process without distraction, free of bureaucratic limitations, and retaining its specialized personnel; 2) sufficient and timely funding coming from national and international sources; and 3) the proactive engagement of federal authorities. International collaboration has proven also to be important, as other countries such as New Zealand have vast experience in this subject.

This particular eradication project will benefit many desert island plants and invertebrates, seven species of reptiles, more than nine species of seabirds, and fishing bats, and will represent an enormous advance regarding rat eradications in México. There are at least 20 more islands in Mexico where aerial procedures must be implemented in order to eradicate introduced rodents. Keeping and consolidating the current pace, the complete restoration of all 24 remaining Mexican islands with 60 populations of introduced mammals now appears to be a viable strategic goal that will be achievable by 2025.

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DISTRIBUTION AND ABUNDANCE OF HARVEST MICE AND DEER MICE ON SANTA CRUZ ISLAND IN RELATION TO FERAL ANIMAL REMOVAL

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Abstract—Like all of the California Channel Islands, Santa Cruz Island has been strongly impacted by a variety of introduced non-native animal species. On Santa Cruz, non-native sheep (*Ovis aries*) and feral pigs (*Sus scrofa*) formerly occurred in very high numbers. Sheep were removed from 90% of the island by the late 1980s, and from the remaining 10% by 2001. As of 2007, a control program has eliminated feral pigs as well. We surveyed Santa Cruz Island from 2004 through 2006 to evaluate the distribution and abundance of western harvest mice (*Reithrodontomys megalotis*). The trapping methods that we used also provided data on deer mice (*Peromyscus maniculatus*), and we evaluate the current extent, numbers, and habitat occurrence of both species. Harvest mice were formerly known only from Prisoners Harbor and a few isolated locations in the island's Central Valley. Our surveys found them at sites across nearly the entire island, and their abundance is higher at sites for which there are comparative data. Deer mice also appear to have increased in abundance compared to previous surveys. We predict further increases in both deer mice and harvest mice as island habitats continue to recover from the effects of non-native ungulates. Changes may be conspicuous in herbaceous vegetation types that recover rapidly, but will take longer in communities like oak woodlands that regenerate more slowly.

INTRODUCTION

Compared to the adjacent mainland, there are very few small mammal species on the southern California Channel Islands. On five of the eight islands, the only native small mammal is the deer mouse (*Peromyscus maniculatus*). The western harvest mouse (*Reithrodontomys megalotis*) is the only other native rodent and is found on three islands—San Clemente, Santa Catalina, and Santa Cruz (von Bloeker 1967). The San Clemente harvest mice are thought to have been inadvertently introduced in hay bales shipped to the island in the late 1930s, and have always had a limited distribution (von Bloeker 1967). Populations on Santa Catalina and Santa Cruz are believed to be native, and distinct island-endemic subspecies have been proposed for the two islands. Pearson (1951) described *Reithrodontomys megalotis santacruzae* based on its longer body, longer tail, and grayer, "less richly colored" dorsum compared to *R. m. longicaudus* from the California mainland. Genetic, morphologic, and allozyme studies also indicate the San Clemente Island population is a recent arrival and that the Santa Catalina and Santa Cruz populations have been isolated for longer periods, but they do not provide strong support for subspecies recognition (Ashley 1989; Collins and George 1990). Collins and George (1990) suggest that harvest mice probably reached both Santa Catalina and Santa Cruz during Holocene times by inadvertent transport on Native American canoes traveling between the mainland and the islands.

Studies in other areas have noted both lower diversity and abundance of small mammals in grazed versus ungrazed areas (Rosenstock 1996; Steen et al. 2005). These effects may be especially pronounced for murid rodents such as harvest mice and deer mice (Jones et al. 2003). Harvest mice typically live in dense grass and herbaceous vegetation, where they build above-ground nests and feed on seeds and invertebrates (Webster and Jones 1982). Heavy grazing, trailing and flattening of vegetation, and rooting and churning of the soil by sheep, pigs, and other non-native ungulates on Santa Cruz Island (e.g., Klinger et al. 2002) have

probably reduced and degraded suitable areas for harvest mouse foraging, escape cover, and nests. Because of their relatively vulnerable above-ground nests, there may also be direct predation by pigs, particularly on dependent young mice. Changes associated with feral animals may have reduced both the overall distribution and the local abundance of harvest mice on Santa Cruz, and their absence or low numbers seems to reflect this.

On Santa Cruz Island, harvest mice were long thought to be limited to the marsh area at Prisoners Harbor on the north shore of the island (Pearson 1951). However, Bills (1969) trapped a single harvest mouse on a sagebrush-covered hillside in the eastern Central Valley. Collins and George (1990) also found harvest mice in the eastern end of the Central Valley. This area is approximately 3 km straight-line distance from the Prisoners Harbor marsh. Little other information has been published on the population biology or ecology of the harvest mouse on Santa Cruz Island. Because of its evident rarity, the harvest mouse is of particular concern to the land managers of Santa Cruz Island, as feral animal removal efforts have been completed and habitat restoration projects are being undertaken. Here we present information on the overall distribution, abundance, population trends, and habitat associations of the western harvest mouse on Santa Cruz Island, based on three years of field surveys and a review of other published and unpublished small mammal surveys on the island.

METHODS

Work on this project consisted of: 1) intensive trapping in the Prisoners Harbor area; 2) extensive surveys around the island, starting with other locations known to have harvest mouse detections (Central Valley/Valley anchorage area), then expanding to other potential sites across the island; and 3) review of published and unpublished data and reports. The field component examined distribution of harvest mice both at a broad, island-wide scale, and at a microhabitat scale at Prisoners Harbor. We also recorded data on habitat associations of the mice on the island, and evaluated relative abundance and other aspects of the ecology of harvest mice on Santa Cruz Island. We reviewed all published literature and unpublished information on harvest mice and their occurrence and ecology on the island. Unpublished reports and data were found primarily at Channel Islands National Park, the University of California Field Station on Santa Cruz Island, and in field notes housed at regional museums. We also reviewed specimen data at museums with important Channel Islands holdings, including the Los Angeles County Museum of Natural History, the Museum of Vertebrate Zoology at the University of California, Berkeley, the San Diego Natural History Museum, and the Santa Barbara Museum of Natural History.

We used folding aluminum small mammal traps for all field sampling (23 x 9 x 8 cm; H. B. Sherman Co., Tallahassee, FL—use of product name does not imply endorsement by the U.S. Government). Depending on the size of the site we set out from 20 to 100 traps, deployed in transects or grids. Transects typically consisted of 10 stations spaced 10 m apart, with 2 traps per station, for a total of 20 traps. In most cases, the transects were not straight lines, but rather were set out to follow the habitat or feature of interest (e.g., riparian areas along stream courses, or the edge of a marsh area). Grids consisted of 50 to 100 traps, with either 5 rows of 10 traps, or 10 rows of 10 traps, with a spacing of 7 m between traps. We used grids in areas of relatively uniform habitat, and in areas where we were repeating previous trapping efforts. UTM coordinates were recorded with GPS at the beginning and end of transects, or at the corners of grids.

Traps were baited with rolled or crimped oats and placed along the edge of dense vegetation, in small openings in vegetation, or along habitat features that would tend to direct the movements of small mammals (e.g., alongside a fallen log). In some areas, particularly parts of the Prisoners Harbor marsh, we avoided pig trails or areas of extensive pig disturbance. Traps were set in the late afternoon or early evening, and checked early the following morning so that captured animals were in the traps no longer than necessary. On cold evenings, we added cotton batting to the traps for warmth.

We identified trapped animals to species, weighed and measured them, and recorded age and reproductive status. Most sites were only trapped once per trapping session, but at sites that were trapped for two or more nights, mice were marked

with individually numbered ear tags. We followed recommended precautions to minimize exposure to Hantavirus and other mammal-borne diseases. We also noted the general habitat type of each trapping site (e.g., marsh, riparian, grassland, coastal sage scrub), and we recorded detailed habitat notes at each trap station where a harvest mouse was captured, including habitat type, substrate, and species composition and structure of the vegetation. We noted evidence of pig disturbance where it was present. Location information was incorporated into a GIS database.

Trapping effort was recorded as the number of traps set, times the number of nights the traps were open ('trap-nights'). Traps that were noted as non-functional when they were checked (e.g., traps that had closed during the night, or had been robbed without closing), were subtracted from the total number of traps available for that night. Abundance was calculated in terms of capture rate—the number of mice captured, divided by the number of functional traps set in a given area. This calculation of relative abundance is useful for comparison to most other available trapping data for Santa Cruz Island. Previous trapping on the island has consisted of irregular transects or small grids, and the combination of low trap numbers, irregular trap arrangement, and small sample sizes (animals captured) precludes calculating densities with realistic mark-recapture models.

Our fieldwork included 47 sampling sessions, from October 2004 through April 2006. Some sessions were from the same site, or close to the same site, on different dates (Fig. 1; Table 1). Sampling effort totaled 1581 trap-nights (Table 1). Twenty sessions were in the Prisoners Harbor area, with a total of 539 trap-nights. Other areas sampled spanned much of the island, from Scorpion Valley on the east to Black Point Canyon on the west, and from the north side of the island (Prisoners and Scorpion) to the south side (Valley Anchorage and the mouths of Willows and Laguna Canyons; Fig. 1). Habitats trapped included fresh and brackish

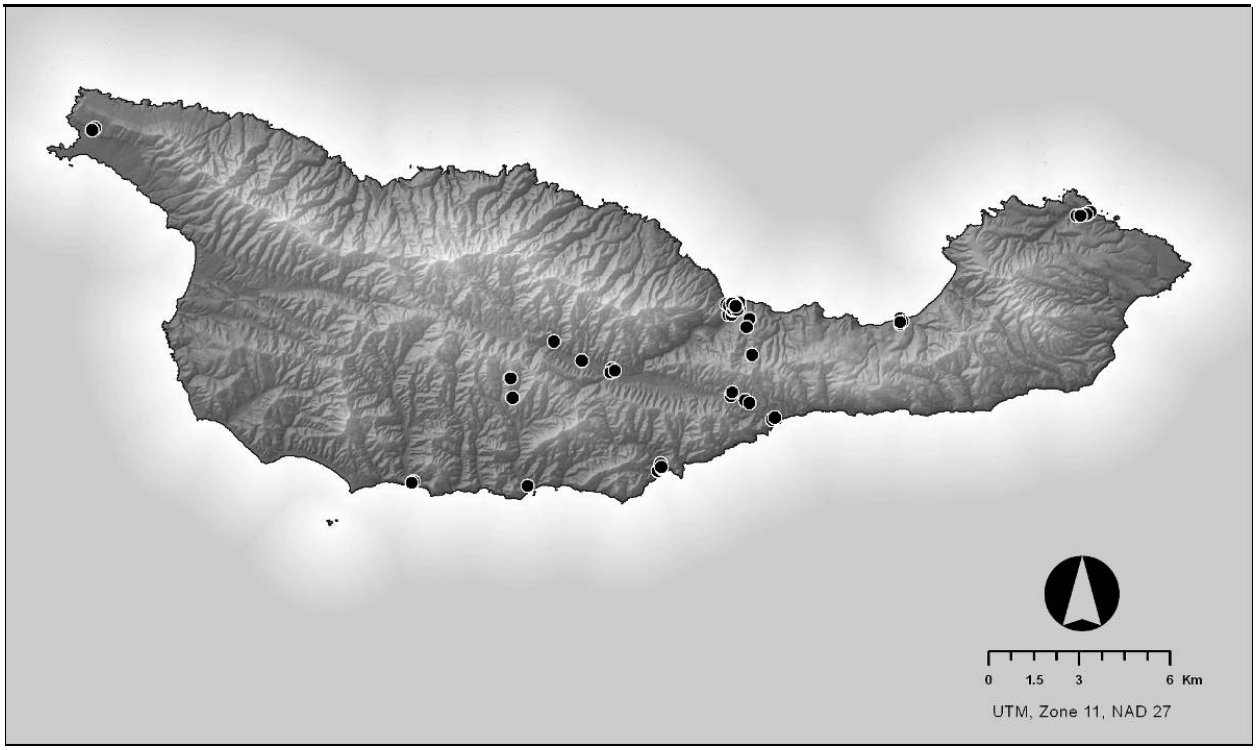

Figure 1. Trapping sites for western harvest mouse (*Reithrodontomys megalotis)* on Santa Cruz Island, California, during a survey conducted in 2004–2006. Multiple sample sites at Prisoners Harbor and Scorpion Valley overlap at this map scale.

Table 1. Trapping effort and capture rates for western harvest mice (*Reithrodontomys megalotis*) and deer mice (*Peromyscus maniculatus*) by date and trap site on Santa Cruz Island, California. Percent capture rates equal the number of individuals captured (harvest mice, deer mice, or total captures) divided by the number of available traps, times 100. In the last row, mean percent capture rate is listed.

			Deer mice		Harvest mice	
Site	Habitat	Traps	Number	%	Number	%
Scorpion Valley	Wet grassland	60	16	26.7	7	11.7
China Harbor	Weedy grassland	38	23	60.5	0	0.0
Valley Anchorage rim	Fennel grassland	17	3	17.6	0	0.0
Valley Anchorage drainage	Chaparral / mixed	18	4	22.2	1	5.6
Lake Pasture (Klinger 78)	Fennel grassland	123	39	31.7	5	4.1
Cañada del Medio, east of airstrip	Fennel grassland	39	6	15.4	0	0.0
Navy Road, just east of Prisoners	Weedy grassland	28	5	17.9	0	0.0
Prisoners Harbor area	Marsh, pasture, riparian	471	120	25.5	33	7.0
Airstrip Coastal Sage Scrub (Klinger 74)	Coastal Sage Scrub	80	15	18.8	1	1.3
Pelican Bay trail	Oak savanna	40	10	25.0	0	0.0
Central Valley (Klinger 23)	Fennel grassland	50	7	14.0	0	0.0
Coches Prietos	Mixed grass / shrub	40	8	20.0	0	0.0
Central Valley near UC Field Station	Mixed grass / shrub	60	0	0.0	0	0.0
Grassland Grid (Klinger 81)	Wet grassland	200	0	0.0	18	9.0
La Cascada—from pool downstream	Mixed grass / shrub	40	8	20.0	0	0.0
Willows Canyon mouth	Mixed grass / shrub	40	17	42.5	1	2.5
Willows Grassland (Klinger 38)	Dry grassland	78	4	5.1	3	3.8
Willows Oak (Klinger 41)	Oak savanna	80	5	6.3	0	0.0
Laguna Canyon mouth	Mixed grass / shrub	40	5	12.5	0	0.0
Black Point Canyon	Mixed grass / shrub	39	10	25.6	0	0.0
Totals:		1581	305	19.3	69	4.4

water marsh, riparian woodland, wet and dry grasslands, coastal sage scrub, and oak savanna.

We specifically targeted harvest mice in our surveys, by searching for and trapping in microhabitats that appeared suitable for this species. This was not the case for most earlier small mammal trapping. For this reason, comparisons with earlier studies may be somewhat misleading. More accurate comparisons can be made where we could re-survey specific sites that were trapped previously. The best data in this respect are those of Klinger (The Nature Conservancy, unpublished), conducted between 1991 and 1995. Klinger established grids of 50 traps in a 5 x 10 configuration at selected sites in a variety of habitats around the island. These sites were all mapped precisely and were sampled in a systematic manner that we could replicate. The data from these surveys are even more valuable because the five-year time span of the work provides a range of potential year-to-year variation in numbers. We relocated Klinger's trapping sites in grassland and fennel – grassland, and also re-trapped other sites where he found harvest mice (oak savanna in Willows Canyon and coastal sage scrub in the eastern Central Valley). We set out the same number of traps in the same configuration at all of these sites.

Comparisons of harvest mouse occurrence among different habitats, and of capture rates between this study and previous surveys, were based on capture rate proportions. We used non-parametric tests (Chi-square goodness of fit and Wilcoxon matched-pairs signed-ranks test, Daniel 1990) with α set at 0.05.

RESULTS

Numbers

We captured a total of 69 harvest mice (overall capture rate of 4.4%) and 305 deer mice (capture rate 19.3%). Numbers of mice caught varied by site and habitat (Table 1). Harvest mouse capture rates varied widely, but ranged up to 22% for some sessions at Prisoners Harbor. The highest overall capture rates for harvest mice were at Prisoners Harbor (7.0%, averaged over varied habitats) and in grass and marshland at Scorpion Valley (11.7%). Capture rates for deer mice were consistently higher at almost all sites, ranging up to 60% in some locations.

We conducted field sampling every other month of the year, with one gap—we did not sample in the month of February. Beginning in October 2004, we sampled in October, December, April, June, and August (2005), then again in April 2006. This nearly year-round schedule provided information on timing of reproduction in harvest mice on the island. Both males and females were reproductively active in April. Four of seven females caught in April were lactating and a single female caught in October was also lactating or had been recently. Two subadults and one juvenile were caught in April and a single subadult was caught in June. Evidence of reproduction or young was not seen in other months.

Distribution

We found harvest mice at eight of our sampling sites on Santa Cruz Island (Fig. 2; Table 1). In addition to Prisoners Harbor, these sites ranged from Scorpion Valley (the easternmost site), the Valley Anchorage area, to the mouth of Willows Canyon. Harvest mice have also been found in the Black Point area at the west end of the island (G. Roemer, personal communication). Locations at Scorpion Valley, Valley Anchorage, the west end of the Central Valley, Willows Canyon, and the Black Point area are previously unreported locations for harvest mice on Santa Cruz Island.

Deer mice were nearly ubiquitous in all sampling areas. We only failed to capture deer mice during two sampling sessions; in December 2004 in the Central Valley near the University of California field station and in April 2006 in the Central Valley (Table 1).

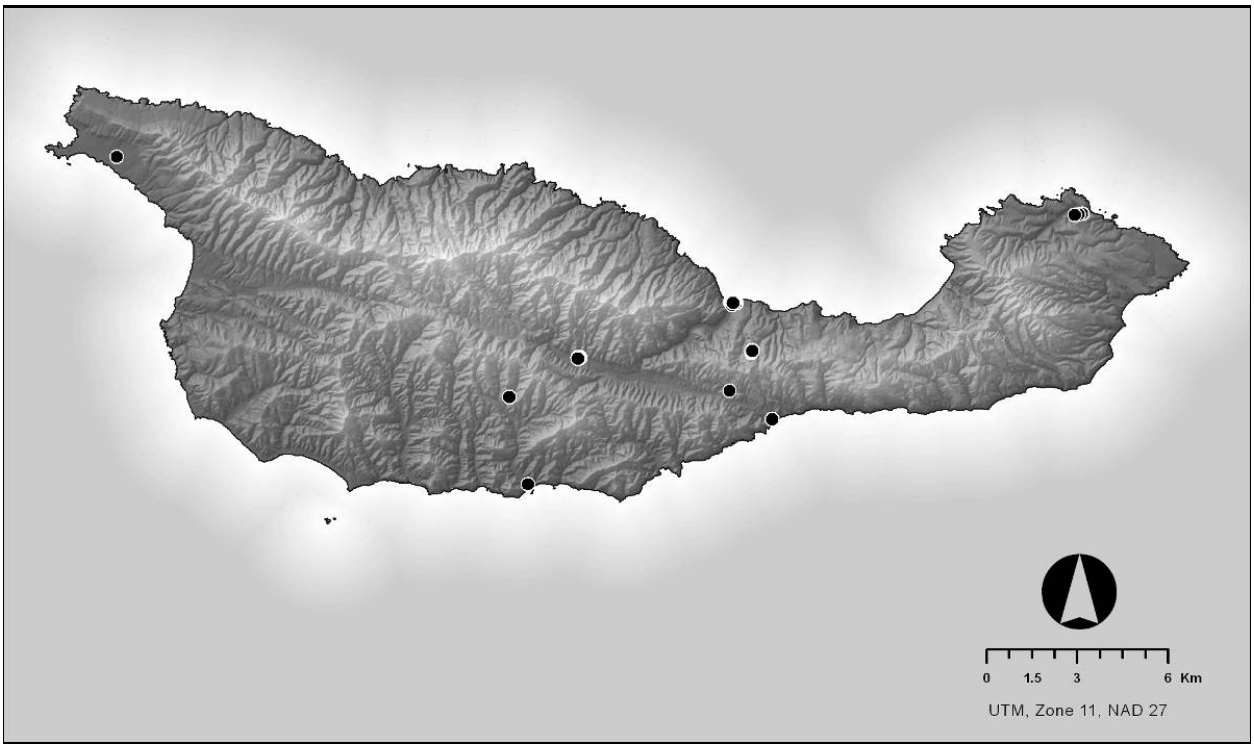

Figure 2. Capture locations of western harvest mouse (*Reithrodontomys megalotis*) on Santa Cruz Island, California, during surveys conducted from 2004 through 2006. In some places (Prisoners Harbor and Scorpion Valley), multiple captures are not shown at this map scale.

Habitat

We captured harvest mice in habitats ranging from *Scirpus* marsh to dry weedy grassland edges and coastal sage scrub. In most cases the microhabitat at trap sites where we caught harvest mice was comprised of dense herbaceous vegetation. Capture rates differed significantly by habitat type (Chi-square < 0.001, n=60, 7 df). Habitats with higher–than-expected capture rates included: 1) a back-beach/marsh-edge vegetation association, which included willow (*Salix* sp.), mule fat (*Baccharis salicifolia*), California bulrush (*Scirpus californicus*), and herbaceous species such as silver beachbur (*Ambrosia chamissonis*), brome grass (*Bromus* spp.), and rabbitsfoot grass (*Polypogon monspeliensis*); 2) wet grassland, including both native (e.g., saltgrass, *Distichlis spicata*) and non-native species (rabbitsfoot grass, ryegrass, *Lolium* sp., and smilo grass, *Piptatherum miliaceum*); and weedy edge habitats, including species such as wild oats (*Avena* spp.), wild lettuce (*Lactuca* sp.), mugwort (*Artemisia douglasiana*), and other herbaceous species. Habitats with lower than expected capture rates included: non-native pasture (kikuyu grass, *Pennisetum clandestinum*); dry grassland, dominated by wild oats and ripgut brome (*B. diandrus*); and coastal sage scrub, with shrubs including coastal sagebrush (*Artemisia californica*), chamise (*Adenostoma fasciculatum*), and mountain mahogany (*Cercocarpus betuloides*), and herbaceous understory of grasses (wild oats, brome), fennel, wild lettuce, and nightshade. No harvest mice were caught in areas with a closed tree overstory.

Previous Surveys

Since Pearson (1951) first documented the occurrence of western harvest mice on Santa Cruz Island, there have been a number of museum collecting trips to the island as well as several studies of small mammal population dynamics, genetics, and disease (Table 2). All of these studies have generally found few or no harvest mice away from the Prisoners Harbor area. Bills (1969) trapped extensively around the island, accumulating nearly 4000 trap-nights of sampling effort in 9 natural habitats and 2 human-associated habitats. At Prisoners Harbor he caught 11 harvest mice in 839 trap-nights (1.3% capture success). At 37 other sites around the island he only caught 1 other harvest mouse, in coastal sage scrub near the airfield in the east end of the Central Valley. Gill (1980) caught no harvest mice in 281 trap-nights at four locations, including 70 trap-nights at Prisoners Harbor.

From 1991 through 1996, R. Klinger (unpublished data) conducted annual trapping at 10 sites in 5 different habitats. During this period he caught only 10 harvest mice in over 8000 trap-nights (0.12% capture success). Five of these were in fennel grassland in Lake Pasture, 1 was in oak savanna in upper Willows Canyon, 2 were in coastal sage scrub in Willows Canyon, and 2 were in coastal sage scrub on the north side of the Central Valley airfield. This last location was in the area where Bills (1969) and Collins and George (1990) had each captured a single harvest mouse. Graham and Chomel (1997) used two trap webs with 200 traps each to sample the main ranch area and the east part of the Central Valley. They caught a single harvest mouse at the east valley site in 1200 trap-nights (0.08% capture success).

Comparison of our grid-trapping results in 2005 and 2006 with Klinger's results from 1991 through 1995 (all years combined) shows a large increase in capture rates of harvest mice (Table 3). Overall capture rate for harvest mice in the earlier surveys was under 0.3%, compared to 4.7% for the later surveys. No harvest mice were captured at Willows grassland and the Central Valley grassland in the 1990s, but these two sites had some of the highest capture rates in 2005–2006. Even with the relatively small number of sites where we could make such direct comparisons, capture rates were significantly greater in 2005–2006 (Wilcoxon matched-pairs signed-ranks test, $n = 5$, $T = 0$, $p = 0.0313$).

We did not make detailed comparisons of deer mice numbers between our surveys and earlier studies. In general, however, deer mice appear to have increased as well. Over all of his trapping sites, Klinger had a capture rate of 11% for deer mice compared to our overall capture rate of 19.3%.

DISCUSSION

Trapping

Harvest mice occur in low numbers at most sites, and we probably failed to detect them at some trap locations where they may have occurred. In areas where we had limited trapping effort (e.g., 40

Table 2. Harvest mouse captures in past small mammal trapping on Santa Cruz Island, California. Listed are date, observer, location of trapping, number of traps set, and trapping results. "Trap effort" is the number of traps set times the number of nights of trapping; "number" is the number of harvest mice caught; and "capture rate" is the number of mice captured, divided by trap effort, times 100.

Bills (1969) – Survey period 1968–1969			
Habitat/Location	Trap effort	Number	Capture rate
Chaparral	624	0	0.00
Outcrop	384	0	0.00
Marsh	839	11	1.31
Riparian	733	0	0.00
Grassland	370	0	0.00
Meadow	105	0	0.00
Sagebrush	180	1	0.56
Pines	360	0	0.00
Buildings	144	0	0.00
Dump	48	0	0.00
Grazed slopes	122	0	0.00
Total:	3909	12	0.31
Gill (1973/unpublished notes) – Survey period fall 1973			
Beach / Riparian – Coches	30	0	0.00
Stream / Riparian – Central Valley	148	0	0.00
Prisoners Harbor	70	0	0.00
Buildings / Stanton Ranch	33	0	0.00
Total:	281	0	0.00
Klinger/The Nature Conservancy (unpublished) – Survey period 1991–1995			
Chaparral – Portezuela (plot 84)	750	0	0.00
Chaparral – Willows Canyon (plot 95)	900	0	0.00
Coastal Sage – Valle del Medio (plot 74)	750	2	0.27
Coastal Sage – Willows Canyon (plot 36)	900	2	0.22
Fennel Grassland – Lake Pasture (plot 78)	750	5	0.67
Fennel Grassland – Central Valley (plot 23)	750	0	0.00
Grassland – Valle del Medio (plot 81)	900	0	0.00
Grassland –Willows Canyon (plot 38)	750	0	0.00
Oak Woodland – Willows Canyon (plot 41)	900	1	0.11
Oak Woodland – Matanzas (plot 20)	900	0	0.00
Total:	8250	10	0.12
Mayfield et al. (2000) – Survey period July 1994–March 1995			
Habitat / Location	Trap Effort	Number	Capt rate
Chaparral	1176	0	0.00
Coastal Sage Scrub	1176	0	0.00
Grassland	1176	0	0.00
Fennel Grassland	1176	0	0.00
Oak Woodland	1176	0	0.00
Total:	5880	0	0.00
Graham and Chomel (1997) – Survey period March 1996			
Ranch	600	0	0.00
East Valley	600	1	0.17
Total:	1200	1	0.08

Table 3. Capture rate of harvest mice from six sampling grids on Santa Cruz Island, from 1991 through 1995 (R. Klinger data, from The Nature Conservancy), compared to the same grids in 2005 and 2006. Effort = number of trap-nights, capture rate = number of mice divided by effort, times 100.

	1991–1995			2005–2006		
Location (Grid)	No. mice	Trapping effort	Capture rate	No. mice	Trapping effort	Capture rate
Willows Grassland (38)	0	300	0.00	2	49	4.08
Willows Oak (41)	1	600	0.17	1	109	0.92
Central Valley fennel – grass (23)	0	450	0.00	0	50	0.00
Central Valley Coastal Sage (74)	2	750	0.27	1	80	1.25
Central Valley Grassland (81)	0	150	0.00	18	200	9.00
Lake Pasture fennel / grass (78)	5	750	0.67	5	86	5.81
Total:	8	3000	0.27	27	574	4.70

traps for one night), our failure to find harvest mice does not prove their absence and additional trapping effort would be needed to better ascertain whether harvest mice are present in those areas. Our data show the general extent of distribution on the island, but not the finer details of their occurrence.

Distribution and Numbers

The distribution of harvest mice on Santa Cruz Island is much wider than previously documented. Harvest mice occur from Scorpion Harbor on the east to the Black Point area at the west end of the island, and from the south shore (Willows Canyon and Valley Anchorage) to the north shore (Prisoners Harbor and Scorpion Valley). Based on our trapping, it appears that the species occurs across most or all of the island where there are sufficient areas of suitable habitat. In spite of the number of small mammal studies on Santa Cruz Island, there have been no previous extensive surveys that specifically targeted harvest mouse microhabitat. For this reason, our results probably do not indicate a large expansion in the range of the species. The disjunct distribution of harvest mice across the island suggests that they have been widely distributed in low numbers for some time, but have gone undetected. This evidently relictual pattern of occurrence probably reflects isolation of suitable harvest mouse habitat into restricted pockets. The patchy, but island-wide distribution also supports the long-term presence (i.e., pre-European times) of the species on Santa Cruz Island as suggested by Collins and George (1990).

The design of most of the earlier trapping studies does not allow calculation of population densities. However, we can estimate population trends by comparing relative abundance over time on the basis of capture rate. In 2004–2006, our capture rates of harvest mice were higher than had ever been reported on Santa Cruz Island, averaging 4.4% at individual sites. This is in contrast with earlier surveys, in which all capture rates for harvest mice were less than 1%. Thus, although distribution of harvest mice has probably not increased, our trapping results do indicate an increase in numbers.

Habitat

von Bloeker (1967) described the Prisoners Harbor location where he originally found harvest mice as being similar to harvest mouse habitat on the mainland, consisting of "patches of grass and forbs around springs and small streams, and … marshy areas dominated by growths of tules, bulrushes, and willows." At Prisoners Harbor, we frequently caught harvest mice at the edge of grass/herbaceous habitats and patches of willow and mule fat, but only rarely deep within patches of shrubs. None were captured under continuous tree or dense shrub canopy. We found a small number of harvest mice in the non-native kikuyu grass that blankets large areas in and around the historic corrals near the harbor. However, these occurrences were almost all along edges, where there was a mix of kikuyu and other native and non-native herbaceous plants.

Based on our trapping, harvest mice in the Prisoners Harbor area appear to be nearly or completely restricted to the marsh, parts of the

pasture in and around the corrals, and the back beach area at the harbor mouth, an area of roughly 1 ha (Fig. 3). We did not catch any harvest mice along the forested stream channel that traces the east edge of the Prisoners Harbor valley mouth. We also trapped the beaches and bluffs to the east and west of Prisoners Harbor (on either side of the black outline in Fig. 3, and beyond) and approximately 500 m up the drainage to the south (beyond the area shown in the photo).

Two seemingly unusual habitats at Prisoners that supported numbers of harvest mice were: 1) drier grass and herbaceous habitat in the archaeological exclosure east of the Prisoners Harbor wetland; and 2) the margin between beach sand and the wetland habitat behind the beach. The occurrence of harvest mice within the archaeological exclosure may be influenced by protection offered by the surrounding fence—both for the vegetation and for the mice. The back-beach habitat is different than most areas where we captured harvest mice, with a more extensive shrub canopy (mule fat and willow) and open understory with scattered grasses and such species as silver beachbur. Most of this habitat is adjacent to the Prisoners Harbor wetland and the mice may be using the wetland/beach edge.

Lower Scorpion Valley had one of the highest harvest mouse capture rates of any area on the island. The lower part of Scorpion has broad areas of tall, dense grass (primarily non-native smilo grass, *Piptatherum miliaceum*) with scattered shrubs. Our trapping at this site indicates that harvest mice occur throughout the extent of this dense, moist, low-lying grassland. Similar habitat occurs at the mouths of some other large drainages around the island, and harvest mice are to be looked for in such areas.

Harvest mice on Santa Cruz Island are also present in some drier upland areas, either in tall, thick grasslands, or in coastal sage scrub with intermixed grass and herbaceous vegetation. In coastal sage scrub, we captured harvest mice in gullies and small canyons that were wetter and had denser vegetation than the surrounding shrub

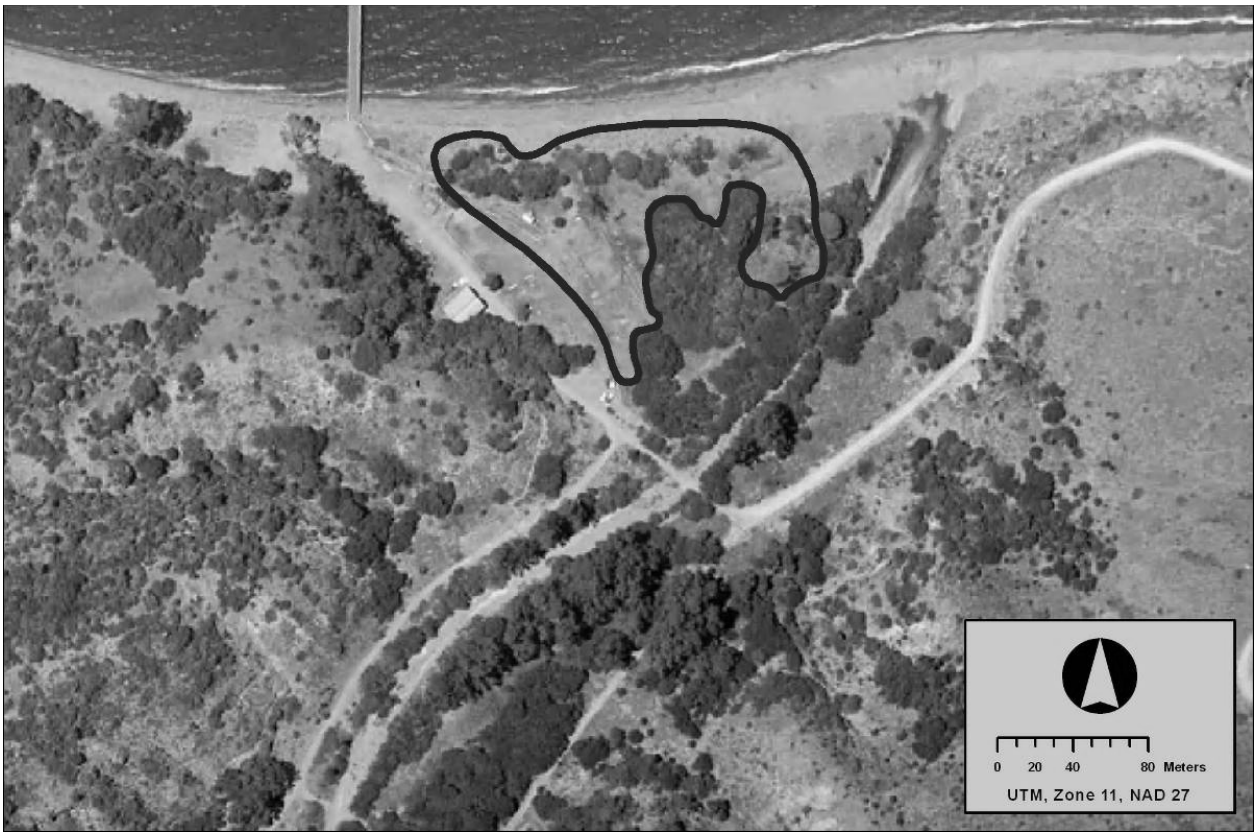

Figure 3. Local distribution of harvest mice at Prisoners Harbor, Santa Cruz Island, California. The broad dark line shows boundary of where harvest mice were captured from 2004 through 2006.

community. Grassland in the west end of the Central Valley where harvest mice occurred had low, boggy areas where ryegrass replaced the wild oats and bromes of drier sites. Such moist microhabitats may be especially important on slopes and hillsides that are otherwise relatively dry and sparsely vegetated.

Feral Animal Effects

Sheep, pigs, and other non-native animals were introduced onto Santa Cruz Island in the mid- to late-1800s. They subsequently increased to very high numbers, with estimates of sheep numbers in the late 1800s ranging up to 60,000 (Brumbaugh 1980). Their grazing, trailing, and other activity on the island was associated with major changes in the vegetation of Santa Cruz Island (Brumbaugh 1980; Junak et al. 1995). Careful descriptions, photographs, and other data from this time period are relatively few and detailed botanical data are lacking. Because of this, our understanding of vegetation changes that occurred is somewhat general in nature, and patchy in its geographic extent. For Santa Cruz Island and the other Channel Islands, however, it is generally agreed that there was widespread reduction of shrub and tree communities, denudation of ground cover with accompanying erosion, and severe losses of some plant species to the point of extirpation (Dunkle 1950; Coblentz 1980; Hobbs 1980; Peart et al. 1994; Junak et al. 1995).

The Santa Cruz Island Company (landowner of the island at the time) began efforts to reduce the numbers of feral sheep starting in 1939 (Junak et al. 1995). The Nature Conservancy assumed partial management of the island in 1978 and began an intensive removal program for sheep in 1981. Sheep were effectively eliminated from the western 90% of Santa Cruz Island by 1989 (Schuyler 1993). The island vegetation communities have shown marked recovery since that time, with increased vegetation cover, higher germination rates of tree and shrub seedlings, and increased numbers of some rare plant species (Schuyler 1993; L. Laughrin, personal communication). Junak et al. (1995) specifically noted increased vegetative cover and amount of water in coastal marshes at the mouths of canyons after the cessation of sheep grazing, and Klinger et al. (1994, 2002) recorded increased herbaceous cover and decreased bare ground in grassland habitat over the period 1984–1993. Greater cover and density of these marsh and grassland habitats should be particularly important for harvest mice on the island.

Santa Catalina Island is the only other member of the California Channel Islands where harvest mice have a long-established native population. In limited trapping on Santa Catalina Island, Perlmutter (1993) found harvest mice to be nearly as numerous as deer mice. Catalina also has more extensive areas of dense native shrub habitats and tall dense herbaceous vegetation. Although Santa Catalina Island still has non-native grazing animals (notably the managed herd of bison [*Bison bison*]), vegetation on that island may provide an indication of the conditions that Santa Cruz Island will tend toward following the removal of sheep, pigs, and other non-native species.

Although they outnumber harvest mice, numbers of deer mice on Santa Cruz Island are lower than on other islands in the Channel Islands group. Deer mouse populations on some of the other islands, particularly Santa Barbara Island (Drost and Fellers 1991), reach extraordinary levels—much higher than deer mouse densities reported anywhere else in North America. During high population periods on Santa Barbara, capture rates frequently exceed 100% (this can occur when individual traps catch two or three mice). Although we did not concentrate on deer mouse populations for this survey, their relatively low abundance may reflect the persistent effects of sheep, pigs, and other non-native animals on cover, food resources, and other habitat requirements (Mayfield et al. 2000).

Management Considerations

Feral pigs on Santa Cruz Island consumed, trampled, and uprooted herbaceous vegetation and young woody plants on the island. Vegetation surveys have found these effects in essentially all habitats on the island, including the grasslands, marsh, and other habitats where harvest mice occur. Up through the end of fieldwork for this study (April 2006), the wetlands and grassland at Prisoners Harbor showed extensive trailing and trampled vegetation from pigs. The control program by the National Park Service and The Nature Conservancy is now complete, and pigs have been eliminated from Santa Cruz Island. Based on what we know of habitat preferences of harvest mice, and of the effects of pigs on vegetation cover, we predict that

both distribution and numbers of harvest mice should increase. Numbers of deer mice on Santa Cruz are relatively low compared to populations on the other Channel Islands, and we expect this species to increase in numbers as well. In some areas, such as the much-reduced coastal sage scrub community and oak woodlands, vegetation recovery and associated changes in small mammal numbers will probably be gradual. In other areas, such as wetland habitats where vegetation regrowth can be rapid, increases in mouse numbers may occur more quickly. The island has been in the process of vegetation recovery since sheep were removed, and removal of pigs should have additional beneficial effects for the flora and fauna, including the harvest mouse.

Continued monitoring of small mammals on Santa Cruz Island should provide useful information on ecosystem changes that occur following the removal of non-native animals. Harvest mice have been of particular interest and concern because of their low numbers and sparse distribution, but deer mice occur much more broadly and changes in their numbers will potentially provide insights into a wider range of habitats. Both species have a high reproductive potential and are likely to respond quickly to expected changes in vegetation and food resources. Deer mice are also an important prey species for the endangered island fox (*Urocyon littoralis santacruzae*; Moore and Collins 1995). As discussed in this report, there is evidence of increased numbers of both harvest mice and deer mice associated with ongoing vegetation recovery on Santa Cruz Island. The data on small mammal populations collected by The Nature Conservancy (R. Klinger, unpublished) provides a substantial baseline for comparison of future changes, and continued trapping on some or all of the grids on an annual basis would provide an efficient monitoring program with broad habitat coverage. With removal of feral pigs now complete, monitoring over the next four to five years may be particularly important in understanding the response of the island ecosystem.

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FACTORS CONTRIBUTING TO SUCCESS OF ISLAND FOX REINTRODUCTIONS ON SAN MIGUEL AND SANTA ROSA ISLANDS, CALIFORNIA

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Abstract—Documented success in the reintroduction of endangered canids is rare. Here, we report on the success of reintroductions for San Miguel Island foxes (*Urocyon littoralis littoralis*) and Santa Rosa Island foxes (*U. l. santarosae*), each of which had been extirpated in the wild by 2000, when the remaining 15 individuals of each subspecies were brought into captivity. From 2003 to 2007, 123 foxes were released to the wild, and were monitored to determine sources of mortality and to estimate annual survival, pup production, and population size. Annual survival increased to 90% on both islands by 2007, and high reproductive success resulted in wild populations of at least 62 on Santa Rosa and 105 on San Miguel. Several factors contributed to reintroduction success. First, survival of island foxes is very high in the absence of predation, and mortality due to predation had been substantially reduced on both islands by removal of most golden eagles (*Aquila chrysaetos*). Second, foxes were released into low-density habitats, which facilitated high reproductive success and rapid population growth. Finally, release plans included contingencies to address potential predation impacts, and post-release monitoring allowed management decisions to be supported by comparison of wild and captive fox demographic parameters.

INTRODUCTION

Although reintroduction of extirpated species to formerly occupied range is intuitively appealing as a recovery action, the overall success of reintroductions has not been high (Armstrong and Seddon 2007). This is especially true for endangered canids, which have an extremely low reintroduction success rate (Ginsberg 1994; Boitani et al. 2004). In particular, captive-raised carnivores have lower post-release survival than translocates (Jule et al. 2008). Canid reintroductions have been hampered by a number of obstacles, including low survival of captive-born individuals (African wild dogs [*Lycaon pictus*]; Gusset et al. 2008), behavioral variation among captive-raised individuals (swift foxes [*Vulpes velox*]; Bremner-Harrison et al. 2004), hybridization with other species (red wolves [*Canis rufus*]; Kelly et al. 2004), and conflict with and persecution by humans (Mexican wolves [*Canis lupus baileyi*]; Paquet et al. 2001; Povilitis et al. 2006). A handful of canid reintroduction programs have reported success, and these include gray wolves (*C. l. nubilis*) in the Northern Rockies and greater Yellowstone area (Sime and Bangs 2007), and swift foxes in Canada (Carbyn et al. 1994) and Montana (Ausband and Foresman 2007). Here we argue that the reintroduction of island foxes (*Urocyon littoralis*) from captivity to San Miguel and Santa Rosa islands is also a successful canid reintroduction, and we discuss factors responsible for the apparent success.

Island foxes are endemic to the California Channel Islands, and the six largest of the eight islands each support a unique subspecies of fox (Grinnell et al. 1937). Island foxes on San Miguel (*U. l. littoralis*) and Santa Rosa (*U. l. santarosae*) declined catastrophically in the mid-1990s due to predation by golden eagles (*Aquila chrysaetos*; Roemer et al. 2001a; Coonan et al. 2005b). By 2000 the Santa Rosa and San Miguel fox subspecies had each declined to 15 individuals (Coonan et al. 2005a), leaving captive breeding and reintroduction as the only option for recovery of these two island fox subspecies. Captive facilities were established by the National Park Service (NPS) on both islands,

and the remaining foxes were removed from the wild and brought in to these facilities. Precipitous island fox declines also occurred on Santa Cruz (Roemer et al. 2001a) and Santa Catalina islands (Timm et al. 2002), and captive breeding programs were established on Santa Catalina Island by Santa Catalina Island Conservancy and Institute for Wildlife Studies, and on Santa Cruz Island by The Nature Conservancy and NPS. Fortunately, foxes were never extirpated from the wild on those islands, and translocations and reintroductions occurred with existing wild populations of at least 100 on Santa Catalina and 65 on Santa Cruz Island. In contrast, when reintroductions began on Santa Rosa and San Miguel, foxes had been absent from the wild for several years, and the captive populations had grown from the original 15 foxes to above 50 individuals on each island.

Because the San Miguel and Santa Rosa island fox subspecies, along with those on Santa Cruz and Santa Catalina, were listed as endangered in 2004 by the U.S. Fish and Wildlife Service (USFWS), the ultimate measure of reintroduction success might be the achievement of recovery criteria and the de-listing of those taxa. However, such definitions, which as yet do not exist for island foxes, incorporate administrative as well as biological recovery milestones. A more purely biological definition of canid reintroduction success was recently proposed (Boitani et al. 2004), under which reintroduction success is characterized by a) breeding by the first wild-born generation; b) a 3-year breeding population in which recruitment exceeds adult death rate; and c) establishment of a self-sustaining population. We herein present the results of island fox releases from 2003 to 2007 on San Miguel and Santa Rosa islands, and assess the success of those reintroductions in light of these definitions.

MATERIALS AND METHODS

Study Area

San Miguel and Santa Rosa islands are respectively the smallest (38.7 km^2) and second-largest (216.0 km^2) of the six California islands where island foxes occur. Both islands are managed by the NPS, although San Miguel is owned by the U.S. Navy. San Miguel is primarily a gently sloping plateau with long, sandy beaches along the coastline. The island is fully exposed to the prevailing northwesterly wind and is recovering from a period of severe overgrazing and erosion caused by historic sheep ranching (Hochberg et al. 1979). Grasslands cover much of the island, and include both native bunchgrasses (*Nasella pulchra*) and introduced annuals such as *Avena* spp. and *Bromus* spp. Some grassland areas have been colonized by shrubs such as coyote brush (*Baccharis pilularis*), and thick stands of giant coreopsis (*Coreopsis gigantea*) intermix with grasses in many areas. The dominant shrub community is *Isocoma* scrub, characterized by low-growing plants up to 1 m high. No trees occur on San Miguel Island.

The larger size, higher elevations, more varied topography, and unique land-use history of Santa Rosa result in vegetation associations not found on San Miguel. Santa Rosa is instead characterized by a central highland dissected by drainages; a relatively gentle marine terrace occurs north of the highland, whereas steep, deeply incised drainages comprise much of the south portion of the island. Nonnative annual grasslands cover about two-thirds of the island, although native perennial grasses are increasing in distribution. Common scrub communities include coastal sage (*Artemisia californica*) and baccharis (*Baccharis pilularis)* scrub. Island chaparral, characterized by *Arctostaphylos* spp. and *Adenostoma fasciculatum,* is found on the slopes of the central highland and at South Point, and less than 1% of Santa Rosa is covered by woodlands. As on San Miguel, the vegetation on Santa Rosa Island is recovering from the impacts of a history of grazing. A sheep ranching operation in the latter half of the nineteenth century gave way to cattle grazing, which occurred from the early twentieth century until 1998. Non-native mule deer (*Odocoileus hemionus*) and elk (*Cervus elephas*) were also brought to the island early in the last century for hunting, and currently exist at population levels of 400–1000 each.

All of the Channel Islands are subject to a Mediterranean climate regime characterized by cool, wet winters and warm, dry summers. On Santa Cruz Island, where there is a 102-yr record, average precipitation is 50 cm/year (Bakker et al. 2009), but with significant annual variation due in part to the El Niño/Southern Oscillation phenomenon. Some

annual precipitation occurs in the form of fog drip, particularly on San Miguel Island.

Release Methods

Between 2003 and 2007, foxes were released to the wild during the fall (October–December). By this time the young of the year have grown to adult size and begin dispersing from their natal areas (Moore and Collins 1995). Conditions under which foxes were kept in captivity have been previously described (Coonan et al. 2005a). Foxes were released as groups of unmated animals, as pairs of potential mates, as pairs that had previously been housed together in captivity for up to one year, and as family groups (siblings or parent-sibling groups). Animals released as potential mates were housed together for 7–14 days prior to release.

Foxes were released at sites that had no or little fox use, as indicated by radiotelemetry of collared foxes, and were known to have been utilized by foxes prior to the establishment of the captive breeding programs. Releases occurred in the late afternoon in areas providing substantial vegetative cover. Foxes were released using a modified hard-release methodology, meaning that foxes were not acclimated to their release areas in temporary pens prior to release, but were released directly from crates. Foxes were supplementally fed after release to ease their transition to the wild, to enhance initial survival, and to encourage released animals to stay in or near their release sites (Kleiman 1996). Remote feeding stations were placed near the release sites, and were subsequently moved in some cases dependent upon the actions of individual animals. Feeding stations were supplied daily with dog kibble for the first month, and then three times a week for the next two weeks.

Prior to release each fox was outfitted with a 38-g radio-collar (M1930, Advanced Telemetry Systems, Inc., Isanti, MN; or MI-2, Holohil Systems Ltd., Ontario, Canada) fixed with a mortality sensor to allow for tracking, mortality monitoring, and potential recovery of animals from the field if necessary. Radio-collars were also affixed to a portion of the wild-born foxes captured during fall trapping (see below) in years subsequent to initial release of foxes into the wild, in order to track survival and mortality causes for the recovering populations. The ultimate goal was to maintain at least 40 active radio-collars on each island, because that was the number required to detect mortality rates of 0.025 with 95% confidence (Doak 2007). Thus, on San Miguel the number of collared animals was 84 (61 released foxes and 23 wild-born) and 82 on Santa Rosa (62 released foxes and 30 wild-born).

Each released fox was tracked on a daily basis for the first month after release, three times per week during the second month, and then at least once per week for the remainder of the year following release. If a mortality signal was detected, the carcass was recovered as soon as possible and sent to the Veterinary Medical Teaching Hospital, University of California–Davis for necropsy. Foxes were determined to have died from golden eagle mortality if they possessed any of the following characteristics: evisceration, degloving of limbs, talon marks, or presence of eagle feathers and whitewash (uric acid) at the carcass site (Roemer et al. 2001a; Coonan et al. 2005b). In 2003 and 2004 foxes were trapped one month after release to check general body condition and weight. If a trapped fox had lost > 20% of its release weight, it was returned to captivity until it had gained back enough weight to be re-released.

Locations of radio-collared foxes were determined by triangulation or by visual confirmation. Coordinates of each visually confirmed location were recorded with a geographic positioning system (GPS) device (Garmin International, Inc., Olathe, KS), as were locations from which triangulated bearings were obtained. A minimum of three bearings was used to determine locations by triangulation using program LOCATE II (Pacer Computing, Truro, NS, Canada). Likely den sites were identified when the locations of radio-collared females became consistent over a 2-week time period in one location during early to mid-April, and remote camera stations were then set up near these sites in early summer (when pups emerge from dens) to record the number of pups weaned from each litter. Each camera station included a box trap (23 X 23 X 66 cm, Tomahawk Live Trap Co., Tomahawk, WI), wired open and baited with dog kibble. A digital camera (Digital Scout, Penn's Woods Products, Inc., Export, PA) recorded fox activity in or near the trap when triggered by a passive infrared detector. Assignment of adult pair members to each camera site was determined by overlap of their female ranges with those of males, direct observation of males and

females traveling together, and visual identification of individuals at camera stations.

Wild fox populations were monitored annually from October through January via transect trapping (both islands) and small grids (San Miguel only). Box traps were baited with dry and wet cat food and a fruit scent (Knob Mountain Raw Fur Co., Berwick, PA), and a polyethylene tube chew bar was wired inside each trap to reduce incidence of tooth damage. Upon first capture, animals were weighed in the trap, and then removed and handled without anesthesia to collect data on sex, reproductive status, age class, and general physical condition (e.g., condition of coat, presence of ectoparasites, injuries). Captured foxes that had not been released or captured previously were marked with passive integrated transponder (PIT) tags (Biomark, Boise, ID) inserted subcutaneously between and just anterior to the scapulae.

Data Analyses

Annual survival of radio-collared foxes was estimated with the non-parametric Kaplan-Meier procedure. This analysis derives cumulative survival in a time period based on the cumulative mortalities and the staggered entry of foxes into the sample as they were released to the wild, and of wild-born foxes as they were radio-collared (Pollock et al. 1989). For each island, survival was thus estimated for a pooled sample comprising both adults and juveniles, and released and wild-born individuals. We determined the minimum number of foxes known to be alive (MNKA) annually on San Miguel and Santa Rosa Island via transect trapping (both islands) and small grids (San Miguel only), in concert with data from radiotelemetry. Other population estimation methods, such as estimation of density from grids, are appropriate at medium to higher fox population levels (Roemer et al. 1994) and although we began such density estimation on San Miguel in 2006, those data are not included here because we do not have comparable data from Santa Rosa. The MNKA was estimated as the sum of the number of individuals caught during fall trapping and the number of radio-collared individuals not caught during trapping but known to be alive via regular telemetry monitoring. We estimated λ, the annual rate of population growth, included the captive facilities, and subsequent interactions between captive and wild foxes resulted using the equation $\lambda = \frac{MNKA'_{t+1}}{MNKA_t}$, where $MNKA'_{t+1}$ is the *MNKA* for year *t*+1 minus the number of foxes released in year *t*+1. Results from annual trapping were used to estimate reproductive success as the ratio of pups to the number of adult (>1 yr old) females. We compared reproductive effort to islandwide population size, including those data from the period of decline (1993–1998; Coonan et al. 2005b), to assess the relationship between density dependence and reproductive effort.

For the 123 foxes released from 2003–2007 on Santa Rosa and San Miguel islands, we also used logistic regression (SYSTAT 10, SPSS Inc., Chicago, IL) to determine if fate of released foxes (dead or alive) was affected by island, age of fox at release, or sex.

RESULTS

From 2003 to 2007, 123 island foxes were released to the wild on San Miguel (n = 61) and Santa Rosa (n = 62) islands (Fig. 1). Releases began a year earlier (2003) on Santa Rosa than on San Miguel (2004), because the captive population on Santa Rosa reached the target captive population size (40 foxes or 20 pairs) sooner on that island (Coonan et al. 2005a). Of the seven foxes released in 2003 on Santa Rosa, five were captured and returned to captivity because their home range

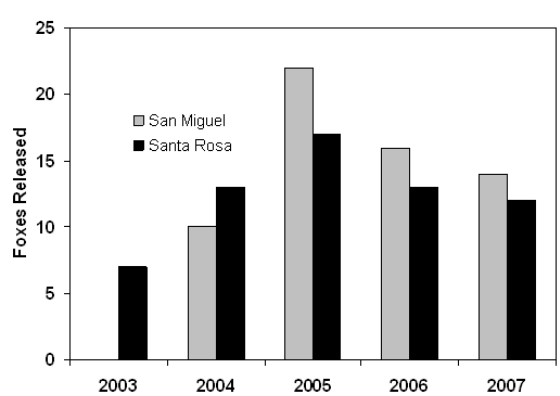

Figure 1. Number of island foxes released annually on San Miguel Island (total = 62) and Santa Rosa Island (total = 62), 2003–2007.

Table 1. Annual minimum number of foxes known to be alive (MNKA) on San Miguel and Santa Rosa islands, calculated as the sum of the number of foxes trapped and the number of additional foxes known to be alive via radiotelemetry, and annual rate of population growth (λ).

	Trap nights	No. trapped	On air[a]	MNKA	Adjusted MNKA[b]	λ
San Miguel						
2004		--	10	10		
2005	252	23	17	40	18	1.8
2006	458	72	8	80	64	1.6
2007	471	83	22	105	91	1.1
Santa Rosa						
2003		--	7	7		
2004	513	15	--	15		
2005	309	20	12	32	15	1.0
2006	887	38	2	40	27	0.8
2007	681	49	13	62	50	1.3

[a] Number of additional foxes known to be alive via radiotelemetry.

[b] Annual MNKA – number of foxes released that year.

in injuries to four individuals. The fifth animal was returned to captivity due to unacceptable weight loss and then was re-released within two weeks.

The minimum number known to be alive (MNKA) increased on both islands, and by 2007 was greater than 100 on San Miguel and greater than 60 on Santa Rosa (Table 1). The annual rate of population growth (λ) on the two islands ranged from 0.8 to 1.8, and averaged 1.2.

Annual survival ranged from 34 to 93% on Santa Rosa, where 33 radio-collared foxes died, and 84 to 100% on San Miguel, where 12 radio-collared foxes died (Fig. 2). Golden eagle predation was the most common mortality cause, accounting for 13 of the 45 mortalities (Fig. 3). No mortalities due to predation occurred in the final year of the study period, by which time 44 eagles had been removed from the northern Channel Islands, with only 1 possibly remaining (Table 2; Latta et al. 2005; Institute for Wildlife Studies 2006). Santa Rosa foxes also incurred mortalities in 2006 due to various factors not related to predation (intestinal intussusception, cholecystisis with septicemia, aggression-caused wounds, and entrapment in irrigation pipes; Coonan et al. 2007).

Results of logistic regression analysis indicated that island ($t = 3.166$, $p = 0.002$) and age at release ($t = -2.703$, $p = 0.007$) affected survival of released foxes, whereas sex ($t = 0.784$, $p = 0.433$) did not. Foxes released on San Miguel were 1.9 times as likely to survive as foxes released on Santa Rosa. Younger released foxes were more likely to survive than older foxes; odds of surviving declined by 20% with each additional year of age. Of the 39 released foxes that died during the study period, over half (20) died within three months of release, a period which coincided with the highest golden eagle activity (winter-spring).

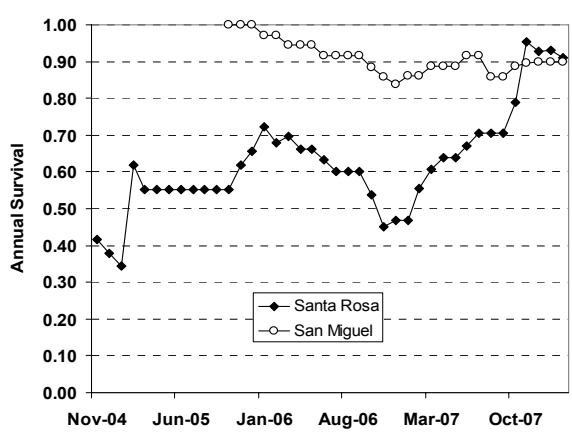

Figure 2. Annual survival of released and wild island foxes on San Miguel and Santa Rosa Islands, 2003–2007. Each point represents annual survival for the previous 12 months.

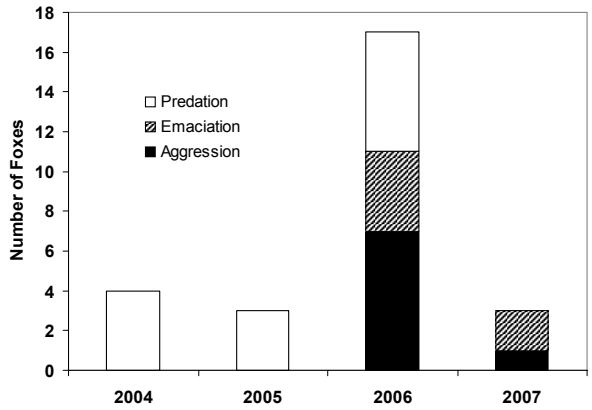

Figure 3. Mortality causes for radio-collared island foxes on San Miguel and Santa Rosa Islands, 2003–2007.

Released and wild-born foxes produced at least 119 pups, including 74 on San Miguel and 45 on Santa Rosa, as indicated by the number of pups trapped during annual population monitoring (Table 3). Remote camera monitoring of selected pairs in 2005 and 2006 revealed that 74% of monitored pairs produced pups (Table 4). Reproductive success was higher on San Miguel (94%) than on Santa Rosa (50%). Camera data indicated that eight of nine released females on San Miguel bred in the wild after release, whereas only three of eight did so on Santa Rosa.

Foxes in the wild reproduced at a fairly young age (Table 4). All of the females released on San Miguel in the fall of 2004 were juveniles, and all produced litters the following spring. In subsequent years at least 10 juveniles born to released foxes also bred and produced litters at the end of their first year. Reproduction by the first generation of wild-born individuals occurred on both islands. Seven successful breeding pairs from both islands included at least one individual born the previous spring; and for two successful pairs on San Miguel, both the male and the female were born in the wild the previous spring. The reproductive success by juvenile foxes, both released and wild-born, stands in contrast to that recorded on San Miguel prior to the decline, when only 19% of juvenile females bred successfully (Coonan et al. 2005b).

The average number of pups produced by monitored pairs was greater on Santa Rosa ($\bar{x} = 2.9$, $n = 7$) than on San Miguel ($\bar{x} = 2.2$, $n = 16$), though this difference was influenced by the occurrence of one very unusual five-pup litter on Santa Rosa in 2005. The ratio of pups to adult females from annual trapping data varied from 0.4 to 2.5 (Table 3). On San Miguel Island productivity was inversely correlated with islandwide population size (Fig. 4), suggesting a density-dependent birth rate.

DISCUSSION

In 2001 island foxes were absent from the wild on San Miguel and Santa Rosa. By 2007, within three to four years after initial releases to the wild, island fox populations on San Miguel and Santa Rosa islands could be characterized as established, recovering populations, due to high survival, high reproductive success, and subsequent high annual rate of growth. The apparent success of the reintroductions is corroborated by application of the reintroduction success standards proposed by Boitani et al. (2004). First, breeding by the first wild-born generation, as evidenced by remote camera observations, occurred quickly on both islands. Some foxes released from captivity bred in the first spring following fall releases, particularly on San Miguel, and many pups produced by released foxes also bred at the end of their first year.

Table 2. Number of golden eagles removed from the northern Channel Islands, and estimated number of golden eagles remaining, after annual capture efforts in 2000–2007.

	Eagles removed	Eagles remaining
2000	13	10
2001	6	8
2002	3	14
2003	9	13
2004	7	11
2005	3	3
2006	3	2
2007	0	1
Total	44	

Data are from Latta et al. 2005; Institute for Wildlife Studies 2006; and D. Garcelon, Institute for Wildlife Studies, unpublished data.

Table 3. Wild pups captured during annual trapping efforts, and ratio of pups to adult females trapped, on San Miguel and Santa Rosa islands, 2005–2007.

	San Miguel		Santa Rosa	
	Pups	Pups/ adult female	Pups	Pups/ adult female
2004	--	--	2	0.4
2005	10	2.5	9	1.0
2006	37	2.5	21	2.1
2007	27	1.4	13	0.76
Total	74		45	

Second, recruitment exceeded adult death rate on both islands over a three-year period, as reflected in average lambda.

The third reintroduction success factor of Boitani et al. (2004) is the establishment of a self-sustaining population, a condition best evaluated with demographic modeling. Recent demographic modeling (Bakker and Doak 2009; Bakker et al. 2009) suggests that at the present 90% survivorship, a sustained population size of as few as 150 yields acceptable extinction risk. As of 2008 the San Miguel population had met this demographic goal and at current levels of recruitment and survivorship, the Santa Rosa population may reach this demographic target within several years (T. Coonan, unpublished data).

Population growth rates were higher on San Miguel, due to both higher survival and higher reproductive success. Santa Rosa foxes suffered higher predation due to the continued presence of golden eagles, which bred on Santa Rosa but never on San Miguel (Latta et al. 2005). The lower reproductive success on Santa Rosa may be attributed to the Allee effect (difficulty in finding mates at low densities). Recent demographic modeling found evidence for Allee effects in island fox population dynamics (Bakker et al. 2009). Santa Rosa's larger size may have made it more difficult for released foxes to find mates. Foxes traveled farther from release sites on Santa Rosa than on San Miguel (T. Coonan, unpublished data).

The success of these initial releases of island foxes to the wild on San Miguel and Santa Rosa islands bodes well for eventual recovery of those two subspecies, and we identify five factors common to both islands that have contributed to this success: 1) mitigation of the primary mortality factor; 2) release location and habitat quality; 3) high reproduction at low densities; 4) comprehensive monitoring of released animals; and 5) a flexible adaptive management strategy. We discuss each of these factors below.

Reduced Predation

The primary reason for the recovery of island fox populations was the early detection and mitigation of eagle predation, the primary cause of fox mortality. Eagle removal eliminated this catastrophic mortality factor, increased fox survivorship, and allowed reintroduction to succeed. By 2007, virtually all the golden eagles present at the beginning of the decline had been removed from the islands or had left of their own accord (Latta et al. 2005; Institute for Wildlife Studies 2006). From 1999 to 2004 a total of 31 adult golden eagles were removed from Santa Cruz and Santa Rosa islands, with a corresponding increase in wild fox survival on Santa Cruz from 61% to >80% (Coonan et al. 2005a) as well as the increase in survival on Santa Rosa, documented in this study. During the study, golden eagle presence and breeding supported by an alien prey base were the substantial differences between Santa Rosa and San Miguel. For species naïve to diurnal predators (Roemer et al. 2001b), the presence of even a few golden eagles tips the balance toward decline (Bakker et al. 2009). On San Miguel, in the absence of eagles, natural productivity was extremely high, and annual survival was over 90% (Fig. 2).

Minimizing eagle impacts on foxes in the long run may ultimately depend on removing the factors that attract and support them there. Golden eagle presence on the islands was facilitated by an alien prey base—feral pigs on Santa Cruz Island and mule deer on Santa Rosa Island (Collins and Latta 2006). By 2008 significant progress had been made toward changing the ecological conditions that allowed golden eagles to persist on the northern Channel Islands. The eradication of feral pigs on Santa Cruz Island is complete (Morrison et al. 2007), but mule deer will remain on Santa Rosa Island until their scheduled removal in 2011. As long as this food source persists on the island it could continue to draw golden eagles from the mainland. Golden

Table 4. Breeding success of radio-collared wild fox pairs on San Miguel (SMI) and Santa Rosa (SRI) islands, 2005–2006, as determined by remote cameras.

Island	Year	Pair#	Female	Born	Age	Male	Born	Age	Pups
SMI	2005	M0501	F302	Captive	1	M203	Captive	3	2
SMI	2005	M0502	F301	Captive	1	M201	Captive	4	2
SMI	2005	M0503	F303	Captive	1	M206	Captive	2	4
SMI	2005	M0504	F304	Captive	1	M205	Captive	1	2
SMI	2006	M0601	F301	Captive	2	M201	Captive	5	1
SMI	2006	M0602	F302	Captive	2	M203	Captive	4	1
SMI	2006	M0603	F304	Captive	2	M205	Captive	2	3
SMI	2006	M0604	F303	Captive	2	M206	Captive	3	1
SMI	2006	M0605	F305	Captive	3	M202	Captive	4	2
SMI	2006	M0606	F308	Captive	4	M209	Captive	3	0
SMI	2006	M0607	F313	Captive	2	M214	Captive	4	2
SMI	2006	M0608	F306	Captive	3	M223	Wild	1	2
SMI	2006	M0609	F309	Captive	1	M210	Captive	1	4
SMI	2006	M0610	F311	Wild	1	M208	Captive	1	1
SMI	2006	M0611	F310	Wild	1	M207	Captive	3	4
SMI	2006	M0612	F316	Wild	1	M222	Wild	1	2
SMI	2006	M0613	F315	Wild	1	M218	Wild	1	2
SRI	2005	R0501	F118	Wild	1	M09	Captive	1	3
SRI	2005	R0502	F106	Wild*	6	M05	Captive	3	2
SRI	2005	R0503	F111	Captive	4	M06	Captive	3	0
SRI	2005	R0504	F104	Captive	2	M08	Captive	2	3
SRI	2006	R0601	F104	Captive	3	M08	Captive	3	5
SRI	2006	R0602	F118	Wild	2	M09	Captive	2	4
SRI	2006	R0603	F103	Captive	4	M02	Captive	5	1
SRI	2006	R0604	F111	Captive	5	M06	Captive	4	0
SRI	2006	R0605	F125	Captive	3	M12	Captive	5	0
SRI	2006	R0606	F107	Captive	3	M20	Wild	1	0
SRI	2006	R0607	F109	Captive	4	M18	Captive	6	0
SRI	2006	R0608	F126	Captive	5	M14	Wild	1	0
SRI	2006	R0609	F129	Wild	1	M19	Captive	1	2
SRI	2006	R0610	F121	Wild	1	M10	Captive	1	0

*1 of 15 foxes brought into captivity in 2000, successful founder.

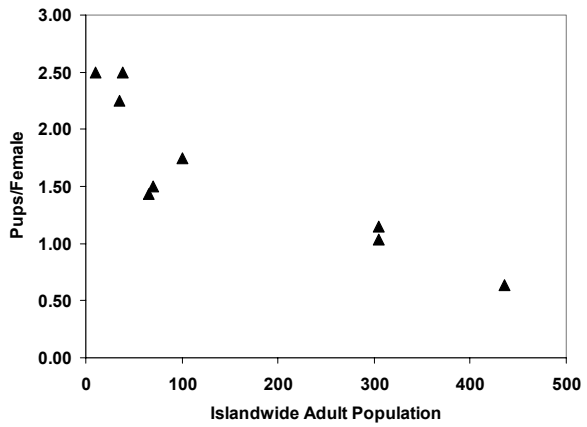

Figure 4. Island fox reproductive effort (pups/adult female) and islandwide population size, San Miguel Island, 1993–2007.

eagles may be discouraged from remaining long on the islands' recovering population of bald eagles (*Haliaeetus leucocephalus*), which were reintroduced to the northern Channel Islands from 2002 to 2006. Bald eagles compete with golden eagles for territories, and do not prey as heavily on island foxes (Buehler 2000; Collins et al. 2005; Collins and Latta 2006). As of 2008, more than 30 young bald eagles inhabited the islands, and two bald eagle pairs fledged young from nests on Santa Cruz Island in 2006, representing the first successful nesting attempts by bald eagles on the islands in over 50 years (D. Garcelon, Institute for Wildlife Studies, unpublished data).

Habitat Quality

Foxes were released into the core of their historic range (Wolf et al. 1996), habitat that is likely of similar or better quality than when foxes were extirpated. On San Miguel Island, for example, sheep grazing during the last century resulted in extreme reductions in vegetative cover. Since the removal of sheep from the island in 1968, native vegetation communities have increased in distribution, expanding into areas that were previously denuded and covered with sand (Hochberg et al. 1979). This condition provides fox habitat that is likely better now than at any other time in the last 50–100 years, and food resources for foxes (including insects, rodents, and fruits [Moore and Collins 1995]) that are likely more plentiful. Similarly, the removal of cattle from Santa Rosa Island in 1998 likely resulted in increased cover and overall habitat quality for both foxes and small vertebrate prey. Deer mice (*Peromyscus maniculatus*), a primary food for foxes (Moore and Collins 1995), have reached higher densities on San Miguel since foxes have been absent (NPS unpublished data), a condition that is likely mimicked on Santa Rosa Island. Moreover, the entire range of each subspecies is completely protected as a National Park, and there has been no net loss of habitat area on either island since foxes have been in captivity. Reduction in core habitat size and/or quality, prey availability, and threats from humans have been identified as primary reasons for previous failures of rare species reintroductions (Fischer and Lindenmayer 2000; Woodroffe and Ginsberg 2000; Moehrenschlager and Macdonald 2003; Van Zant and Wooten 2003; Steury and Murray 2004), but none are a factor for released foxes on San Miguel and Santa Rosa islands. Conversely, the ability of the habitat at this point to provide substantial resources appears to be excellent, resulting in rapid population increase and high survival. For example, on San Miguel Island, the number of foxes in the wild in 2007 was 105, approximately one quarter of the total population estimated to exist on the island prior to the decline (Roemer et al. 1994).

Absence of Competition and High Reproductive Success at Low Densities

The first groups of foxes were released into areas with no conspecifics and were consequently unconstrained in home range establishment. This may be the reason that reproductive success was extremely high not only for released foxes but for their offspring. The reproductive success by juvenile foxes, both released and wild-born, stands in contrast to that recorded on San Miguel prior to the decline, when only 19% of juvenile females bred successfully (Coonan et al. 2005b). Young, inexperienced females may have been able to breed successfully in the wild following release because fox densities were low enough to preclude limitation by lack of territory availability (Roemer et al. 2001b), yet individuals still had access to potential mates because multiple individuals were released at each release site.

Cumulative data from San Miguel populations at all densities from 1993–2007 (10–400/island),

show that reproductive success is inversely density dependent. Given suitable habitat, access to potential mates, and minimal sources of mortality, at low densities the population exhibited extremely rapid growth. As the recovering populations approach carrying capacity, available territories will become scarce, and reproductive success may decline to levels similar to those seen in the early 1990s, at high densities. Nevertheless, the high reproductive success of released and wild foxes at low densities is responsible for quick re-establishment of fox populations. While it is possible that Allee effects (Angulo et al. 2007; Bakker et al. 2009) explain differences between reproductive success on San Miguel and that on Santa Rosa, the overall ability of island foxes to reproduce well at low and medium densities obviates the need for a long-term reintroduction program. In effect, the foxes are recovering themselves.

Monitoring

Comprehensive monitoring of released foxes and wild populations has allowed quick assessment of predation rates, fox survival, and recruitment in the wild, all critical metrics for evaluating the success of releases (Sarrazin and Barbault 1996). All released foxes were radio-collared, as were the majority of the pups born in the wild, and by the end of the study period there were over 80 radio-collared foxes on the two islands. Mortality checks were conducted several times per week, thus providing critical information on predation events and general locations of eagles, and remote camera monitoring and annual trapping proved excellent tools for assessing wild reproductive success. Understanding these dynamics of the recovering wild populations allowed NPS to make informed management decisions regarding the captive breeding and release program, as described below.

Adaptive Management

A recovery approach that includes adaptive management has contributed greatly to the success of the program to date. The formal island fox recovery team established by USFWS was known as the Recovery Coordination Group (RCG) and included individuals from the land management agencies (such as NPS), the USFWS, and non-agency scientists. Management recommendations and requests for information from this group were transmitted through the USFWS to the land-management agencies. For example, by 2003 and 2004 the Santa Rosa and San Miguel captive populations had reached the target sizes at which releases to the wild could be considered, but the prospect of releasing foxes in the presence of golden eagles was controversial (Roemer et al. 2002; Courchamp et al. 2003; Coonan et al. 2004; Roemer and Donlan 2004). The RCG was generally cautious regarding this approach, but the USFWS recommended that releases might be conducted with pre-determined mortality thresholds that, if reached, would require that foxes be returned to captivity. In the spring of 2005, the pre-determined recapture trigger (five predation-caused mortalities) was reached on Santa Rosa Island, but recapture efforts at that time would potentially have separated whelping females from their pups. Accordingly, the USFWS recommended against recapture efforts. Eagle-caused mortalities subsequently ended, and four litters were born in the wild to females that otherwise might have been returned to captivity. The flexibility of such an adaptive approach is critical for a recovery program where management actions are based largely on the results of ongoing monitoring of the released species as well as the behavior of another species, both being factors that can vary considerably within a short period of time.

Decision to Close Captive Breeding

Although the San Miguel captive breeding program produced 53 pups from 1999 to 2006, no pups were produced in 2007 (Coonan and Dennis 2007; T. Coonan, National Park Service, unpublished data). Moreover, from 2005 to 2007 the number of pups produced in the wild was over four times that produced in captivity, and was specifically greater for juvenile females and first-year pairings compared to that in captivity. The lack of breeding by juvenile females in captivity might have been due to social suppression, since mated pairs held in captivity are separated from adjacent pairs by distances of only 3–50 m (C. Asa, St. Louis Zoo, unpublished data). In contrast, the unconstrained mate choice that occurs in the wild likely leads to many more successful pairings than can be "arranged" in captivity. Freedom of movement also allows wild females to avoid injuries due to male aggression during the breeding

season, an occurrence that became increasingly common in the captive populations. The additional problem of neonatal mortality surfaced in the latter years of the captive breeding program. In 2007, comparison of ultrasound results with the number of pups eventually whelped showed that females lost 7 of 14 pups observed on ultrasound on San Miguel and 14 of 21 observed on Santa Rosa (Clifford and Vickers 2007). Some neonatal loss comprised late-term abortion, which is rare in canids, and underlying causes may have included bacterial infection due to reduced maternal immune response, perhaps mediated through stress (C. Asa, St. Louis Zoo, unpublished data). These captive reproductive problems were never resolved.

Given the apparent difference in productivity, by 2007, maintaining foxes in captivity, as opposed to allowing them to reproduce in the wild, was no longer a sound investment strategy for island fox recovery, at least on San Miguel Island. Accordingly, in 2007 all the remaining captive foxes (save two very old females) were released on San Miguel and the facility was closed. In fall 2008 the Santa Rosa captive breeding program was also closed, and all remaining foxes (except for two considered unreleasable) were released to the wild. As on San Miguel, the reproductive rate in the wild had greatly exceeded that in captivity. Ceasing captive breeding marked the achievement of one practical measure of reintroduction success, in addition to the biological milestones presented in this paper.

By 2008, the MNKA for Santa Rosa was 122 foxes, and the population estimate for the San Miguel subspecies, derived from mark-resight efforts on four small grids, was 172 adults, with an additional 100 pups (Coonan 2009). This put the San Miguel subspecies at biological recovery, as determined by comparison to population modeling-derived recovery criteria (Bakker and Doak 2009), and represented an eightfold increase in the Santa Rosa subspecies since its nadir in 2000. Less than 10 years after the remaining 15 individuals from each subspecies had been removed from the wild for captive breeding, both subspecies were recovered or recovering, fully in the wild. Compared to other canid species, there were fewer impediments to recovery for the island fox. They reproduced adequately in captivity and spectacularly in the wild following release, perhaps due to their relatively simple mating system compared to wolves and African wild dogs. No economic development or commercial activity such as ranching was hampered by their recovery; their entire range was managed by conservation organizations; and most importantly, the primary mortality factor was effectively mitigated. Island fox recovery was perhaps most similar to that of reintroduced swift foxes in Montana (Ausband and Foresman 2007), where mortality from predation was overcome by high reproductive success to produce increasing populations. The calculated risk of island fox releases had paid off: though eagle predation had not been completely mitigated when releases began in 2003, high reproduction by released foxes and the resulting quick establishment of wild populations justified that calculated risk.

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IMMEDIATE EFFECTS OF WILDFIRE ON ISLAND FOX SURVIVAL AND PRODUCTIVITY

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Abstract—Island foxes (*Urocyon littoralis*) exist as six endemic subspecies, one on each of the six largest California Channel Islands. All six subspecies are listed as threatened by the California Department of Fish and Game; four of these, including those on Santa Catalina Island, are also listed as endangered under the federal Endangered Species Act. Six wildfires have been documented on the east end of Catalina Island since the endemic fox (*U. l. catalinae*) population underwent a precipitous decline in 1999. An extensive island-wide trap/mark/recapture effort had been carried out annually on Catalina Island from 2001 through 2008 to monitor island fox population status. We compared pre- and post-burn data from foxes captured in traps within and surrounding the burn areas of the two largest fires—the Empire Fire, a 1063-acre lightning-ignited fire on July 22, 2006, and the Island Fire, a 4760-acre accidentally ignited fire on May 10, 2007. Individual survival and pup presence were the main indicators used to measure the immediate effects of each fire. Though overall fox numbers have increased on the east end of the island, a slight decrease in total foxes captured post-fire was observed in both the Empire Fire (18 pre-fire, 16 post-fire) and the Island Fire (42 pre-fire, 37 post-fire) sampling areas. The ratio of pups to adults captured in the Empire Fire sampling area remained similar pre- and post-burn (1:3 and 1:4 respectively) and consistent with the overall ratio observed on the entire east end of the island (1:4). The ratios of pups to adults observed in the Island Fire sampling area pre- and post-burn (1:2 and 1:17 respectively) suggest a possible decrease in fox productivity in the Island Fire zone. A fire event that occurs while pup mobility is limited (April–June) may alter productivity in the affected area by disrupting parturition and weaning, or causing direct mortality, yet may be less critical during other times of the year.

INTRODUCTION

Island foxes (*Urocyon littoralis*) exist as six endemic subspecies, one on each of the six largest California Channel Islands (Gilbert et al. 1990; Wayne et al. 1991). Due to precipitous fox population declines, four of these six subspecies, including the Catalina Island fox (*U. l. catalinae*), have been listed as endangered under the federal Endangered Species Act. Research has suggested that an outbreak of canine distemper virus in 1999 was the probable cause of the fox decline on Catalina Island (Timm et al. 2000). An extensive island-wide trap/mark/recapture and vaccination effort was initiated in response to the decline and had been carried out annually on Catalina Island from 2001 through 2008 to monitor the status of the population recovery. The Catalina Island fox population was estimated at only 784 animals in 2008 (King and Duncan 2008), therefore evaluation of all potential risks to fox survival is necessary to direct ongoing management decisions and assist in setting recovery goals for all four endangered Channel Island fox populations. The potential immediate effects of wildfire on island foxes has not been well documented and though fire is not considered a major threat on its own, information from this study may be useful in determining cumulative risks and modeling population viability.

Fire affects animals at the individual, population, and community levels. The ecological relationship between fire and animal communities is poorly understood, and there is little known about fire effects on the majority of species existing in California (Shaffer and Laudenslayer 2006). Most research into the effects of wildfire on wildlife has focused on mainland populations of small mammals, reptiles, and birds. For relatively small vertebrates, fires can and do cause substantial mortality, and can result in local declines or

extinctions in areas following a fire (Wirtz 1974; McClure 1981; Peek 1986; Patton 1992). Despite these potential population impacts for small vertebrates, most researchers agree that at the regional population level, mortality effects are very small if not negligible (Wirtz 1977; Quinn 1979; Patton 1992). Although there is a potential for a significant local mortality for some species of small animals, a number of species such as the closely related gray fox (*Urocyon cinereoargenteus*), are capable of retreating from oncoming flames, even if they remain within the immediate burn area (Peek 1986; Patton 1992).

Of all fire regime attributes, seasonality of fire may have the greatest potential for affecting individual animal populations. Island fox parturition and rearing takes place during the spring and early summer (April–June), prior to the general California fire season occurring in late summer and early autumn (August–November) (Laughrin 1977; Shaffer and Laudenslayer 2006). Pups emerge from their natal den at 3–4 weeks of age with the majority being seen in early June. By late summer, pups are highly mobile and abandon their dens to forage with their parents daily in preparation for dispersal by autumn (Laughrin 1977).

With the continued increase in island residents, visitors, and interior activities on many of the California Channel Islands, there is a greater potential for human-caused fires to become ignited outside of the traditional fire season. This may result in significant pup mortality if fires occur during a time when pups are in dens and are unable to flee from oncoming flames. Non-seasonal fires may also negatively impact native plant species and local vegetation communities, thereby producing considerable short-term and long-term wildlife displacement due to habitat alteration (Shaffer and Laudenslayer 2006).

The recent (ca. 100 years) fire history on Catalina Island is relatively well documented. Based on personal interviews, newspaper articles, and Los Angeles County and Catalina Island Conservancy records, current information suggests that approximately 40 fires larger than 0.02 km^2 (5 acres) have been documented on Catalina Island between 1915 and 2007. Only one of these fires was ignited naturally via lightning. More recently, six fires have been documented in the interior of the island since the fox decline in 1999. Two of these fires, the Empire Fire, a 4.3-km^2 (1063-acre) lightning-ignited fire on July 22, 2006 and the Island Fire, a 19.26-km^2 (4760-acre) accidentally ignited fire on May 10, 2007, collectively burned 23.56 km^2 (5823 acres), or approximately 12% of Catalina Island (Catalina Island Conservancy, unpublished data 2007).

A significant advantage of this study was that we were able to monitor marked foxes both before and after a fire event within the fire-affected areas (local level) as well as at a population level. This was fortuitous and resulted from a unique set of circumstances. The timing of the two fire events examined in this study also allowed us to compare the immediate effects of fire on foxes during the sensitive parturition season and compare the results to those from a less vulnerable time of the year.

Using annual island-wide trapping data and capture trends, our objectives were to: (1) assess the abundance of marked foxes before and after each fire event at the local and population levels; (2) compare the abundance of fox pups and the ratios of pups to adults before and after each fire event at the local and population levels; (3) compare the ratios of males to females before and after each fire event at the local and population levels; and (4) attempt to assess apparent survival of specific marked adults based on their recapture post-fire.

MATERIALS AND METHODS

Study Area

Santa Catalina Island (approximately 194 km^2) is located approximately 32 km from the mainland (Palos Verdes Peninsula, CA), is 34 km long, and ranges from 1 km wide at the Two Harbors Isthmus to 13 km wide near the center of the island. The isthmus geographically separates Catalina into two distinct sides, the east end and west end. The island is quite mountainous with elevations ranging from sea level to 670 m. Catalina Island has a mild and dry climate with infrequent storms occurring mainly between November and April. Annual precipitation in the city of Avalon averages 314 mm (12.36 inches) with average daytime temperatures ranging from 17 C to 23 C. Predominant vegetation types include coastal sage scrub, coastal bluff scrub, island chaparral, island woodland, riparian

woodland, and coastal grassland (Schoenherr et al. 1999).

The two largest fire events selected for this study included the Empire Fire, a 4.3-km^2 (1063-acre) lightning-ignited fire that occurred from July 22–25, 2006, and the Island Fire, a 19.26-km^2 (4760-acre) accidentally ignited fire that occurred from May 10–15, 2007. The total area burned during the Empire Fire was calculated by walking the burn area perimeter while collecting line function data using a Trimble Geo Explorer 3 GPS unit (D. Knapp, unpublished data). Line data were post-corrected using Pathfinder software from base files accessed through a local base station. Data were exported as a shapefile and total area was calculated using ArcView 3.2. The Island Fire perimeter was digitized from aerial photographs taken on June 7, 2007 by I.K. Curtis Services, Inc., at a scale of 1:30,000. Data were converted to a shapefile and total area was calculated using ArcGIS 9.1.

Trapping

Data gathered during multiple annual island-wide trapping events were used to determine fox abundance, individual fox presence, apparent survival, and pup to adult ratios during periods before and after each fire event. The capture and handling methods used annually on Catalina Island were originally established and implemented in 2000 by the Institute for Wildlife Studies (IWS) while contracted by the Catalina Island Conservancy and have been continued by the Catalina Island Conservancy since the IWS contract concluded at the end of 2005. For the purposes of this study, fox ID, sex, and age class were selected from capture history data associated with the 604 trap sites used each year during 2003–2008. The annual trapping effort was divided into 12 to 13 separate trap lines, consisting of 30 to 60 trap sites and occurred from mid-July through mid-October. Foxes were captured with single-door live traps (Model #106, 23 x 23 x 66 cm; Tomahawk Live Trap Co., Tomahawk, WI) baited with dry cat food, wet cat food, and a loganberry lure (Knobb Mountain Fur Co., Berwick, PA). Captured foxes were weighed (± 25g), sexed, and aged. Age was determined by the relative wear of the first upper molar (Wood 1958; Collins 1993) and foxes were placed in one of five age classes: pups (age class 0), juveniles/young adults (age class 1), adults (age class 2), mature adults (age class 3), and older adults (age class 4). All foxes which had not been previously captured as well as those which had been caught previously and only marked with ear tags, were permanently marked with a passive integrated transponder tag (PIT tag; Biomark Inc., Boise, ID). PIT tags were inserted under the skin between and just anterior to the scapulae using a sterile single-use syringe (King and Duncan 2008).

Isolating Fire-Affected Traps

Geographic information system (GIS) software (Environmental Systems Research Institute, Redlands, CA) was used to create a 500-m buffer around each trap site used annually on the east end of Catalina Island (454 of 604 trap sites). We assumed an "effective trap radius" of 500 m (Schmidt et al. 2005) based on the approximate mean home range size for island foxes on San Clemente Island, California (Schmidt et al. 2004b) and a cursory analysis of home ranges of translocated foxes on Santa Catalina Island (Schmidt et al. 2004a). All trap sites used annually on the east end of the island were collectively placed into the East End category. To quantify potential population impacts resulting from the fires and compare those to the impacts at the local level, the capture history for all trap sites used during annual trapping efforts on the entire east end of Catalina Island were assessed. The remaining 150 of 604 trap sites located on the west end of the island were not included in this study.

Trap sites were placed into either the Empire Fire or Island Fire category if a trap buffer overlapped with, or was located within, the burn area perimeter of either fire event. A history of fox captures occurring between 2003 and 2008 at each trap site was assessed to identify the number of uniquely marked foxes that may have been present within the fire-affected areas before and after each fire.

We calculated the sampling area within the Empire Fire and Island Fire perimeters as the entire area covered (minus overlap) by the 500 m buffers placed around all traps then clipped to the perimeter of each fire, leaving only the buffered area lying inside the appropriate fire perimeter to be calculated. The area sampled for the entire East End was calculated as the area covered (minus overlap)

by the 500-m buffers placed around all 454 trap sites used annually on the East End of Catalina Island.

Adult and Pup Abundance and Ratios

Fox abundance was calculated as the number of individual foxes, pups and adults, captured in each category of traps (Empire Fire, Island Fire, East End) in the years preceding and following each fire event. The ratios of pups to adults within each category post-fire were also calculated and compared to pre-fire ratios using chi-square analysis (GraphPad software 2002–2005). The timing of the annual trapping effort, mid-July through mid-October, was valuable in this comparison because pups continue to remain in close proximity to their parents during the summer and do not disperse until the fall (Laughrin 1977; Fausett 1982).

To evaluate whether the behavior of nursing mothers (e.g., potentially staying with their dependent young versus fleeing, or returning to their young while hazards remained) would affect their immediate survival in the event of a fire, the ratio of adult females to adult males captured in each category of traps annually was calculated and compared using a chi-square analysis against an expected ratio of 1:1.

Apparent Survival of Marked Foxes

Apparent fox survival within the burn areas was estimated by the post-fire recapture of marked foxes that had been captured in these areas prior to the fire event. Because the number of years that annual trapping was conducted after each fire event differed, only foxes recaptured during one subsequent trapping year were compared to the annual recapture results found during non-fire years.

RESULTS

Isolating Fire-Affected Traps

The number of traps included in each trap category (Empire Fire, Island Fire, and Entire East End) was 34, 69, and 454 respectively (Fig. 1). Using the 500-m buffers clipped with the fire perimeters, approximately 58% of the area burned

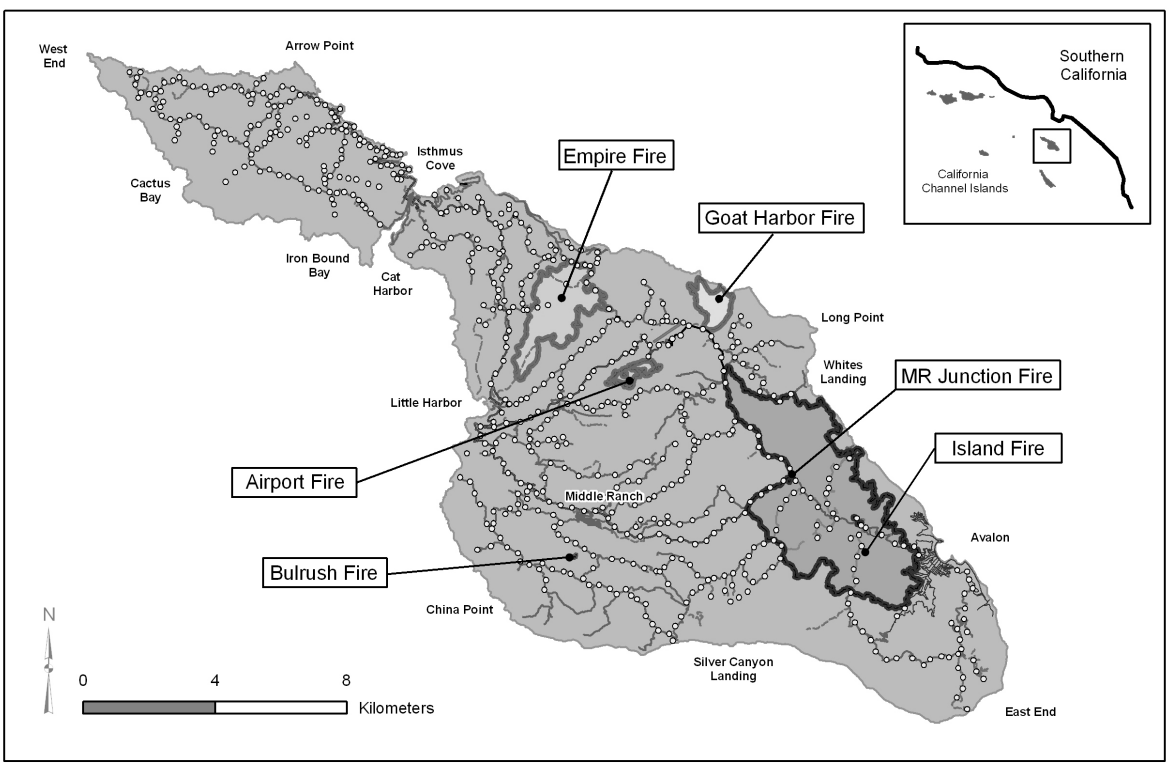

Figure 1. Locations and area of six interior island fires documented on Santa Catalina Island, California between 1999 and 2008. Annual island-wide trap sites maintained from 2003 to 2008 represented by open dots.

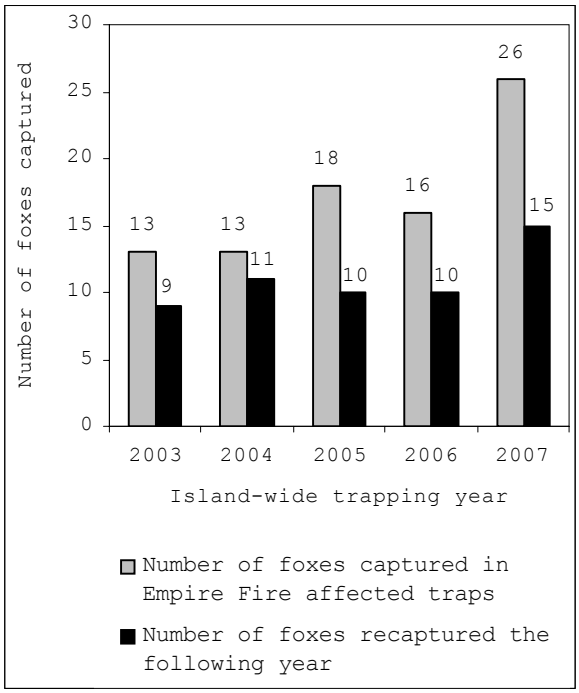

Figure 2. Number of adult foxes and pups captured each year in traps affected by the Empire Fire, on Santa Catalina Island, California from 2003 to 2007. The grey bars indicate the number of foxes captured during the target year and the black bars are the number of those marked foxes captured the following year. The Empire Fire occurred in 2005.

by the Empire Fire and 67% of the area burned during the Island Fire were sampled during each annual island-wide trapping effort. By utilizing the same method of surrounding all 454 East End traps with a 500-m buffer (minus overlap), approximately 71% of the Entire East End of Catalina Island was sampled annually from 2003 through 2008.

Adult and Pup Abundance and Ratios

The total number of foxes captured in Empire Fire-affected traps during annual island-wide trapping decreased slightly from pre-fire sampling (n = 18) in 2005 to post-fire sampling (n =16) in 2006 (Fig. 2). Of the 16 foxes captured within these traps 1 month post-fire, only 7 were from the original 18 detected in this area prior to the Empire Fire. The other 9 foxes detected included 5 new animals (3 pups, 2 yearlings) and 4 marked adults that had either been captured previously during 2004 in those traps, or had been captured during 2005 in a trap immediately adjacent to a fire-affected trap along the fire perimeter line. No previously marked adult foxes were documented to have moved in from outside areas. The ratio of pups to adults captured post-Empire Fire (1:4) did not differ significantly from pre-fire sampling (1:3) ($\chi^2 = 0.22, P = 0.64$) (Table 1). The ratio of adult females to adult males captured after the Empire Fire did not differ significantly from 1:1 ($\chi^2 = 0.078, P = 0.78$).

The total number of foxes captured in Island Fire-affected traps also decreased slightly from pre-fire sampling (n = 42) in 2006 to post-fire (n = 37) sampling in 2007 (Fig. 3). Only 20 of the foxes detected post-fire were from the original 42, while the additional 17 of 37 foxes captured in Island Fire-affected traps during 2007 included 2 new pups, 9 new unmarked adults that had been undetected previously, and 6 marked adults previously captured in traps immediately adjacent to fire-affected traps along the fire's periphery during 2006. Despite an increase in adult foxes present, the number of pups captured in Island Fire-affected traps decreased substantially from pre-fire (n = 14)

Table 1. Number of pups and adult foxes captured in each category of traps during the annual island-wide trapping effort on Santa Catalina Island, California from 2003 to 2008.

		Sampling year					
Area		2003	2004	2005	2006	2007	2008
Empire Fire affected traps (n = 34)	Pups	4	7	4	3	3	19
	Adults	9	6	14	13	23	18
Island Fire affected traps (n = 69)	Pups	0	0	1	14	2	43
	Adults	5	10	12	28	35	33
East End traps (n = 454)	Pups	21	25	42	45	50	157
	Adults	48	89	104	162	196	185

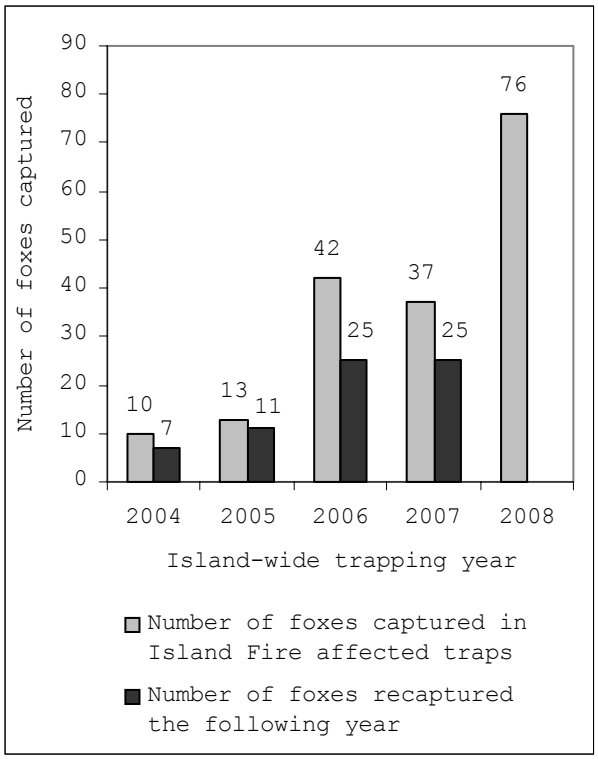

Figure 3. Number of adult foxes and pups captured each year in traps affected by the Island Fire, on Santa Catalina Island, California from 2004 to 2008. The grey bars indicate the number of foxes captured during the target year and the black bars are the number of those marked foxes captured the following year. The Island Fire occurred in May 2007, prior to that year's trapping effort.

in 2006, to 4 months post-fire ($n = 2$) in 2007. This was followed by a substantial increase in the number of pups documented in 2008 ($n = 43$) (Table 1). The ratio of pups to adults differed significantly 4 months post-fire (1:17) compared to ratios documented both before the Island Fire event (1 : 2) ($\chi^2 = 12.33$, $P = 0.0004$) and 1 year following the fire (1:1) ($\chi^2 = 29.43$, $P<0.0001$). The ratio of adult females to males following the Island Fire in 2007 (18F : 17M) did not differ significantly from those ratios documented prior to the fire in 2006 ($\chi^2 = 1.05$, $P = 0.31$) or 1 year after the fire in 2008 ($\chi^2 = 0.12$, $P = 0.73$).

At the population level, the number of adult foxes captured in East End traps during annual island-wide trapping increased each year from 2003 to 2007 despite the Empire and Island Fire events. The number of pups captured in East End traps also increased each year through 2007, but at a slower rate (Table 1). The ratio of adult females to adult males captured on the East End of the island after each fire event did not differ significantly from 1:1 (Empire Fire $\chi^2 = 2.0$, $P = 0.16$; Island Fire $\chi^2 = 0.18$, $P = 0.67$).

The annual variability observed in pup to adult ratios on the East End may best be explained by annual rainfall. The majority of precipitation received on Catalina Island occurs between November 1 and April 30. We found the average ratio of pups to adults significantly lower during dry years (2004, 2006, 2007) when less than 178 mm (7 inches) of rain were recorded, than during wet years (2003, 2005, 2008), when annual precipitation exceeded 305 mm (12 inches) ($\chi^2=25.67$, $P<0.0001$) (Table 2.).

Apparent Survival of Marked Foxes

Of the 18 uniquely marked foxes captured within the Empire Fire-affected traps during 2005, the sample year prior to the Empire Fire, 10 adults

Table 2. Ratio of Catalina Island fox pups to adults captured during annual island-wide trapping on the island's East End. Ratios shown in relation to average annual rainfall received at three weather stations located at Avalon, Middle Ranch, and Airport in the Sky, on Catalina Island, California during 2002–2008.

Rain date range	Pup year	Average rainfall (inches)	Number of pups to adults	Ratio Pups : Adults
November 1, 2002–April 30, 2003	2003	15.24	21/48	1 : 2.3
November 1, 2003–April 30, 2004	2004	6.37	25/89	1 : 3.5
November 1, 2004–April 30, 2005	2005	23.38	42/104	1 : 2.5
November 1, 2005–April 30, 2006	2006	6.84	45/162	1 : 3.6
November 1, 2006–April 30, 2007	2007	3.56	50/196	1 : 4.0
November 1, 2007–April 30, 2008	2008	12.26	157/185	1 : 1.2

and 0 pups (56%) were recaptured during the subsequent post-fire island-wide trapping effort in 2006 (Fig. 2). These foxes may have been captured in any available East End trap to determine apparent survival. This recapture success was not significantly lower than the recapture rates documented in this area prior to the fire in 2003–2004 (χ^2 = 0.33, P = 0.56), or 2004–2005 (χ^2 = 1.29, P =0.25), nor after the fire in 2006–2007 (χ^2 = 0.15, P = 0.69). An additional 5 (3 pups, 2 adults) of the original 18 foxes captured during 2005, yet not detected during 2006, were recaptured the second year (2007) resulting in 15 of 18 (83%) foxes known to have survived at least 1 year after the Empire Fire event. The remaining 3 foxes (1 pup, 2 adults) were undetected during all 3 years of trapping following the fire.

Of 42 individual foxes captured in Island Fire-affected traps during 2006, the sample year before the Island Fire, 25 (60%) were recaptured during the subsequent post-fire island-wide trapping effort in 2007 (Fig. 3). This was significantly lower than recapture results (85%) from trapping efforts in this area during 2005–2006 (χ^2 = 23.53, P = <0.0001), yet not different than the 70% documented from 2004-2005 (χ^2 = 2.195, P = 0.14). Six of the original 42 foxes captured in 2006 were not detected in 2007, yet were recaptured during 2008. Of the remaining 11 foxes not captured in traps during 2007 or 2008, 1 had been radio collared and monitored weekly during 2006 until the collar malfunctioned in June 2007, while a second fox was euthanized in May 2008 due to severe injuries; evidence that these two foxes also survived at least 1 year post-fire. A total of 33 of 42 (79%) foxes therefore were known to have survived at least one year following the Island Fire. The other 9 foxes, (3 pups, 4 new 1-year-olds, and 2 mature adults) were not detected during the 2 subsequent years of post-Island Fire trapping.

Of 146 marked foxes captured on the entire East End of the island during the 2005 annual island-wide trapping effort (before the Empire Fire), 111 (77%) were recaptured the following year (2006). Similarly, of 207 marked foxes captured on the East End during the 2006 island-wide trapping effort (before the Island Fire), 141 (68%) were recaptured during island-wide trapping in 2007 after the Island Fire, suggesting that fire effects were minimal at the population level (Fig. 4). During 6 years of systematic trapping, 2003–2008, we observed a 67% average annual recapture rate of marked foxes on the East End of Catalina Island.

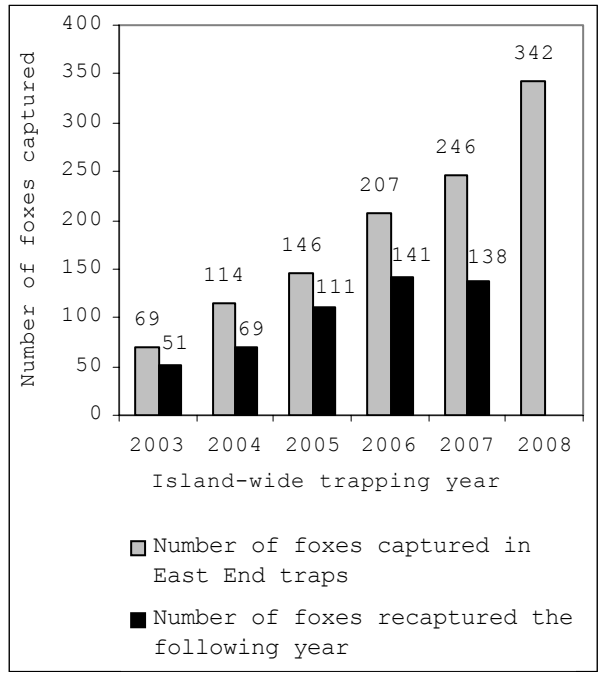

Figure 4. Number of adult foxes and pups captured each year in traps on the East End of Santa Catalina Island, California from 2003 to 2008. The grey bars indicate the number of foxes captured during the target year and the black bars are the number of those marked foxes captured the following year.

DISCUSSION

A fortuitous set of unique factors provided us with an exceptional opportunity to quantify the potential immediate effects of a wildfire event on island fox survival and productivity. The level of monitoring that was in place before either fire event occurred recorded the status of island foxes in each area. Most investigations into the effects of wildfire on wildlife populations have been limited in this regard, as studies are often only initiated after a fire event has occurred (Whelan 1995). We had the rare opportunity to follow marked individuals from a population in which approximately 71% of the overall study area had been systematically sampled for several years prior to and at least two trapping years following each fire event. The timing of the Island Fire also provided us with the ability to gain knowledge of fire effects during the parturition

season (April–June) when foxes are the most vulnerable; this situation would be extremely difficult to replicate both legally and ethically.

Similar to its mainland relative the gray fox, the island fox only uses a den for parturition and pup rearing, which occurs generally from early April to mid-June (Laughrin 1977; Clifford et al. 2007). Island fox dens usually are simple structures that include brush piles, small caves, rock crevices, manmade structures, hollowed limbs or stumps; or, in the absence of existing structures, a simple tunnel may be dug (Laughrin 1977). Most of these types of simple structures would provide little safety in the event of a fire. Other studies that have investigated fire effects suggest that animals taking refuge in burrows or dens may be more susceptible to fire due to extended periods of elevated temperatures and the increased potential for suffocation (Whelan 1995). Captive adult foxes have been documented carrying their young to new den locations within their enclosures. However, it is unknown what behavioral alterations adult foxes would make in the wild during a fire event that took place when pups were completely dependent and had limited mobility. It is possible that due to pup dependence, adult foxes could have remained in or returned to hazardous areas, increasing their chances of injury or death. Several observations of foxes returning to the burn area while flames were still present were documented during the Island Fire. An injured adult female fox showing signs of nursing was also captured and provided with veterinary treatment. Her injuries included severe burns to all four paws suggesting that she may have returned to a hazardous area, perhaps to search for pups, after initially fleeing. This fox made a complete recovery from her burns after extended treatment and was ultimately released back to the wild.

Our comparison of recapture results between annual trapping efforts conducted during years with large documented fire events and those with no fire activity provided no consistent evidence to suggest that either fire event had any influence on the survival of marked adult foxes at the local or population level. As suspected in this case and documented among similar animals, adult foxes had the ability to retreat from the oncoming flames. This was supported with data from 6 adult foxes (3F:3M) fitted with radio collars prior to the Island Fire, which left the affected area during the fire and later returned. All 6 collared animals were monitored weekly prior to and following the fire event for the remainder of the year. All 6 animals survived the fire without injury. We also did not find a significant difference in the ratio of adult females to adult males compared pre- and post-fire suggesting that the behavior of nursing mothers did not influence their survival. If adult foxes were injured or killed within either fire event, is was not at a level distinguishable from the recapture variability documented over several years. Additional post-fire annual trapping efforts would likely detect additional survivors and strengthen the above statements, but the fate of foxes still undetected could not be linked to the fire events.

The similarities in the relative abundance of pups and ratio of pups to adults documented at the local level before and after the Empire Fire (1:3 and 1:4 respectively) would suggest that at the time of this fire (July), fox pups were sufficiently mobile to avoid the oncoming flames and independent enough not to return to the area before the hazards were extinguished. The timing of the Island Fire event however, coincided with the parturition season. The severe decline in the abundance of pups present after the Island Fire and the ratio of pups to adults documented at the local level before and after the Island Fire (1:2 and 1:17) suggests that approximately 10 pups that we would have expected to have captured that year were lost as a direct result of the fire and productivity at the local level was adversely affected.

Our findings indicate that the seasonality of a fire event appeared to have the most influence on immediate fox survival. Fires that occur during early post-parturition may affect survival of pups resident in the fire areas. The negligible effects of either fire event at the population level reflect stability in the current size and structure of the Catalina Island fox population. In situations of poor population condition, including low abundance, restricted age class distribution, or a precipitous decline, a single fire event or a series of fires, as in this case, may pose a serious threat to an animal species or population (Shaffer and Laudenslayer 2006). Although the assessment of the immediate effects of fire on fox survival is important to determine, the long-term fire effects such as habitat alteration and/or conversion to grassland, individual displacement, and resource availability were not

assessed in this study and may prove to have a much larger effect on population recovery.

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BIOMETRIC AND DISEASE SURVEILLANCE OF AN INSULAR POPULATION OF FERAL PIGS ON SANTA CRUZ ISLAND, CALIFORNIA

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Abstract—Feral pigs (*Sus scrofa*) can harbor parasites and other infectious agents that may potentiate sylvatic transmission to native wildlife such as the federally protected *Urocyon littoralis santacruzae* (Santa Cruz island fox) and *Spilogale gracilis amphiala* (island spotted skunk). When the wild boar population on Santa Cruz Island (SCI) was scheduled for eradication, an effort was made to gather reference data on a potential reservoir of parasites and pathogens for future epidemiology and management, should health issues arise among native biota. Blood samples (256) were collected and necropsies (77) were performed to document the health, age, disease exposure, and biometric characteristics of the feral pig population. Samples were conveniently collected during five field visits between July 3 and November 22, 2005 from representative sections of the island. Serum samples were tested for antibodies to *Brucella spp*., pseudorabies virus, *Trichinella spiralis*, *Toxoplasma gondii*, and six serovars of *Leptospira spp*. Tests were negative (with 95% confidence of less than 2.2% prevalence), except for 32 (14%) individuals that had very low antibody titers (1:100–200) to one or more serovars of *Leptospira*. The existence of low antibody titers for *Leptospira* suggests exposure to this agent and perhaps some interaction between feral pigs and other land or sea mammals of the island. Necropsy examination of 77 carcasses was unremarkable. Histologically, mild non-specific background lesions were noted in various organs, interstitial pneumonia being the most commonly seen (38%). No parasites were detected at necropsy from stomach and small or large intestines. Fecal samples from 68 animals examined for parasites/parasite parts detected *Eimeria sp*. oocysts (coccidia, 2.9%), *Demodex sp*. (mite, 2%), and *Metastrongylus sp*. (lungworm, 9%). External parasites that were detected included *Pulex irritans* (human flea), *Ixodes pacificus* (western black-legged tick), and *Haematopinus suis* (hog louse). Data suggests exposure of SCI pigs to several Leptospire serovars that are atypical in pigs. There is no evidence that wild pigs or the eradication efforts on SCI posed a conservation threat to the SCI fox or other SCI species.

INTRODUCTION

The presence of parasites and infectious diseases in Santa Cruz Island (SCI) feral pigs (*Sus scrofa*), which have potential sylvatic transmission to insular wildlife populations of conservation interest such as SCI fox (*Urocyon littoralis santacruzae*) or the island spotted skunk (*Spilogale gracilis amphiala*), has yet to be described. During the decline of the endangered island fox on Santa Catalina Island (SCaI), questions were raised as to whether a particular disease may have been present on the island prior, and particularly if a previously-eradicated non-native species such as the pig could have served as a reservoir for the pathogens. The information presented here on the presence of pathogens on the island and the behavior of these pathogens would be useful in the case of possible future emerging diseases in protected wildlife on SCI. Additionally, human exposure to zoonotic diseases of feral pigs, as well as sylvatic exposure, is potentiated by hunting activities through exposure to carrion (Neiland 1970; Zygmont et al. 1982; Currier 1989; Weigel et al. 1996; Hutton et al. 2006; Lloyd-Smith et al. 2007). The presence of one of these diseases may influence management decisions

during eradication efforts. This project was undertaken to document the health status of a subset of the feral pig population during the process of their eradication. Some background history and potential effects of sylvatic and zoonotic transmission of diseases from of feral pigs are introduced herein.

History

The initial introduction of the feral pig to SCI in 1852 was for commercial purposes. Within the year, the enterprise was abandoned and the pigs went feral (More 1857). Hog cholera (Classical Swine Fever Virus) was purposely introduced on the island three times, once prior to 1944 and at two different times in the 1950s, in an attempt to control or eradicate the pigs with no success (Wheeler 1944; Corn 1987a). In 1987, serologic testing for hog cholera was performed on 31 animals from the SCI pig population and did not detect exposure (APHIS 1987).

Pigs have had multiple biological effects on the island ecosystem, such as competition with native species for food resources (Schuyler 1988), reducing the regeneration of coast live oak (*Quercus agrifolia*) and other woody-species (Peart et al. 1994), and rooting impacts on two rare endemic plants (*Arabis hoffmannii* and *Thysanocarpus conchuliferus*) (Klinger 2003) and seven of the nine listed plant species on SCI (EIS 2002).

Conservation Considerations

This serosurvey was generalized for diseases with sylvatic and zoonotic potential. The inferences for conservation are dependant upon the potential virulence of such diseases in naïve island natives and whether they are passed in carrion. Diseases passed in carrion vary in importance and include pseudorabies virus (PRV) (Weigel et al. 1996), *T. gondii* (Frenkel et al. 1970), *T. spiralis*, *B. abortus*, and *B. suis* (Neiland 1970; Zygmont et al. 1982).

SCI fox have been observed feeding on feral pig carrion; therefore, PRV could be a potentially serious threat to foxes, skunks, and carnivorous birds during eradication activities if the virus was present in the pig carcasses. PRV produces acute disease and high mortality in most non-porcine secondary hosts (E. Hahn, personal communication 2007). PRV has been shown experimentally to be lethal in blue foxes (*Alopex lagopus*), producing an acute illness progressing from anorexia, depression, and coma with meningioencephalitis (Quiroga et al. 1995).

Without the presence of cats (felidae) on the island to shed infective oocysts, a sylvatic transmission cycle of *T. gondii* would depend directly upon carnivorism of encysted meat or nerve tissue (Frenkel et al. 1970). The SCI fox has apparently been living with exposure to *T. gondii* without significant impact on the population. A serologic survey (Garcelon et al. 1992) showed a low antibody prevalence of *T. gondii* in SCI fox, and recent work has shown persistence of the low prevalence in SCI fox of *T. gondii* (Clifford et al. 2006). Although not an apparent conservation threat to the SCI fox, *T. gondii* can infect all warm-blooded animals, including pigs and foxes (Jungersen et al. 2002), and infection in the fox can be asymptomatic or can cause central nervous system or other pathology. *Toxoplasma* was found concurrently with distemper virus in the single fox carcass recovered during the 1999 decline of the SCaI fox (Timm et al. 2009). Recently *T. gondii* and *Sarcocystis neurona* were recognized to cause encephalitis in marine mammals (Dubey et al. 2003). Without adjacent felidae to perpetuate *T. gondii* in the SCI ecosystem, carcasses of marine mammals that beach on SCI should be considered as a potential source of exposure. Marine mammals documented to have *T. gondii* infection include California sea lions (*Zalophus californianus*) (Dubey et al. 2003), harbor seals (*Phoca vitulina*) (Lambourn et al. 2001), and southern sea otters (*Enhydra lutris nereis*) (Kreuder et al. 2003). It has also been recovered from a dolphin fetus (*Tursiops aduncus*) (Jardine and Dubey 2002) and has been isolated from carnivorous birds such as raptors (Lindsay et al. 1993).

Although not a conservation threat, *T. spiralis* can cause myositis, infect both sylvatic and domesticated animals, and be maintained by carnivores such as foxes, skunks, and swine (Murrell et al. 1987). Improper hunting practices contribute to transmission and spread of this infection among wildlife (Pozio 2000). Anaerobic metabolism of the larvae in nurse cells allows their survival in extremely decomposed carcasses. Spread of *Trichinella spiralis* via ingestion of infected musculature is low in swine and high in foxes (Smith 1985).

Although *B. abortus* and *B. suis* have been documented to cause infections in canines (Neiland 1970; Shin and Carmichael 1999), and *B. canis* is known to cause abortion in canids, the effects of *B. canis* and *B. suis* on canids have not been reported to be a direct cause of death. (Neiland 1970). The abortive effects of these strains on canids are in question (Woodroffe and Ginsberg 1997); therefore, these strains of *Brucella* are not considered to be a major conservation threat to the island fox.

Leptospirosis is an acute febrile zoonosis infecting a broad range of mammalian hosts and is re-emerging globally (Lloyd-Smith et al. 2007). It is generally accepted that the major mode of transmission of leptospirosis is by exposure to contaminated water or animal tissues. The various serovars of *L. interrogans* differ widely in their host interactions (Lloyd-Smith et al. 2007). The epizootic infections typical of *Leptospira* tend to be periodic (Gulland et al. 1996). These cycles may be suggestive of either host susceptibility, climactic change, and increase in population density of reservoir hosts and/or "accidental" hosts (Gulland et al. 1996). A central tenant of the epidemiology of leptospirosis is the distinction between maintenance hosts and accidental hosts for a given serovar, or equivalently, between host-adapted and non-host-adapted serovars (Lloyd-Smith et al. 2007). Classically, maintenance hosts develop a chronic, largely asymptomatic infection in their kidneys, and may shed leptospires in their urine for months or years, while accidental hosts experience acute infections with symptoms ranging from malaise to multi-organ failure and death (Lloyd-Smith et al. 2007). There is also a recognized co-adaptation on the part of *Leptospira* strains. Typically there are host-adapted and non-host-adapted strains of leptospires. Host-adapted strains cause mild disease, abortion, a high percentage of seropositives in the host population, and are shed in the urine for long periods (Heath and Johnson 1994; Gulland et al. 1996). Non-adapted strains cause sporadic severe disease in the host, low prevalence of seropositive hosts, and are usually only shed for short periods by host individuals (Gulland et al. 1996). In addition, the behavior of *Leptospira* is often geographically specific, so that within a geographic region, certain serovars are prevalent and become adapted to a particular maintenance host (Bolin and Cassells 1992). Species and epidemiological investigations involve differentiating between maintenance-host populations and accidental-host populations for the serovar in a particular ecosystem (Hathaway 1981). Characteristics of infection with a particular serovar are often considerably different in different hosts; consequently, leptospirosis is more likely to pose a conservation threat when it cross-infects to a new species host, because it is often more virulent in the accidental host. For instance, domestic dogs are considered maintenance hosts for *L.i.* serovar Canicola, and incidental hosts for the other serovars (Moore et al. 2006). A common example of this phenomenon of increased virulence in an incidental host is the (recent) resurgence of acute and chronic leptospirosis in domestic canines, most often caused by *L.i.* serovars of Grippotyphosa or Pomona (Brown et al. 2003). Some of the recent thinking on *Leptospira* epidemiology hypothesizes that an accidental host may sometimes become a maintenance host through a process of an epidemic, when the survivors of the infection sometimes co-adapt and "non-host-adapted" serovars may become "host-adapted" (Gulland et al. 1996; Lloyd-Smith et al. 2007). Therefore, it may be important to know about the existence of reservoirs of leptospires, what the typical maintenance hosts and the actual maintenance hosts may be, and how the organisms are behaving in an ecosystem where managers are seeking to protect and conserve threatened or endangered species.

In the relatively insular environment of SCI, the possibilities of hosts are limited. There are only four indigenous land mammals on the island: deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), spotted skunk, and SCI fox (L. Laughrin, personal communication 1991). Only very few cattle remain localized on the island today, but in the past, cattle, sheep, and pigs were wide-ranging. The sheep (Schuyler 1988) and nearly all the cattle were removed by the early 1990s. The pigs are now considered eradicated. Seals and sea lions, primarily *Phoca vitulina* (harbor seal) and *Zalophus californianus* (California sea lion), with occasional *Mirounga angustirostris* (Northern elephant seal) and vagrants "haul out" on SCI beaches. Carcasses of other marine mammals, *Enhydra lutris* (California sea otter), *Eschrichtius robustus* (California gray whale), and others may

occasionally wash up on SCI beaches. Eight species of bats (Brown 1980) should also be considered as a source of exposure of SCI natives to potential pathogens.

Because of the behavior of *Leptospira* organisms, there are many literature citations of maintenance and incidental hosts that parallel SCI species. The pig has been considered a primary maintenance host for *L.i.* Pomona (Hathaway 1981). In North America striped skunks (*Mephitis mephitis*) are recognized as maintenance hosts for this serovar as well (McKeever et al. 1958; Kingscote 1986). Leptospirosis due to *L.i.* Pomona, has been reported in a small sample of red foxes in Canada causing severe hemorrhagic disease. In this study, the fox appeared to be functioning as an amplifier (accidental) host but not as a maintenance host (Kingscote 1986). *L.i.* Pomona infection is affecting the survival of California sea lions and is thought to have important consequences on population dynamics of the species (Gulland et al. 1996). Although the pig is not considered a primary host for *L.i.* serovar Icterohaemorrhagiae, it was the most prevalent of eight serovars tested in wild swine in Texas (Corn et al. 1986). The rat is considered the primary host for *L.i.* Icterohaemorrhagiae (Ward et al. 2004). Dogs are considered maintenance hosts for serovar Canicola (Moore et al. 2006). Skunks and rats are thought to serve as incidental hosts for *L.i.* Canicola (Roth et al. 1961; Ward et al. 2004) and it has been reported in bats (Matthias et al. 2005) and in other canids. Raccoons are considered to be a primary maintenance host to *L.i.* Grippotyphosa. Skunks have also been cited as showing evidence of exposure to this serovar (Richardson and Gauthier 2003). This was also the most common serovar seen in foxes in Germany (Müller and Winkler 1994). Although cattle are maintenance hosts for *L. borgptersenii* serovar Hardjo, pig, horse, and sheep are also known to carry the infection (Hathaway 1981). *L.b.* Hardjo has also been detected in bats in the Amazon (Matthias et al. 2005). The domestic pig is considered the primary host for *L.i.* serovar Bratislava (S. Hietala, personal communication 2007).

Pulex irritans and *Ixodes pacificus* are thought to be "host-sharing" with the SCI fox and spotted skunk (Crooks et al. 2001; Crooks et al. 2004). *P. irritans* is a possible vector for wild canid disease such as plague (McGee et al. 2006). *I. pacificus* has been known to infest deer mice, western harvest mice, wild turkey (*Meleagris gallopavo*; Lane et al. 2006), and the island fox) (Castro and Wright 2007) and is an important vector of *Borrelia burgdorferi*, the causative agent of Lyme disease. Lyme disease has been reported to cause multisystemic lesions in foxes in Hokkaido, Japan (Isogai et al. 1994). Since Lyme disease does not tend to be epizootic, it represents a low threat to conservation efforts.

Zoonoses

Feral swine carry several diseases that pose a zoonotic threat to humans. Human exposure to carcasses after a hunt can potentiate infections such as brucellosis (from *B. abortus* and *B. suis*) (Currier 1989) leptospirosis (Lloyd-Smith et al. 2007), toxoplasmosis, trichinosis, and sarcoptic mange (Hutton et al. 2006). Lyme disease may also be transmitted to humans via *I. pacificus* (Burgdorfer et al. 1985).

MATERIALS AND METHODS

To maximize sample yield, five field sample periods were performed in conjunction with early trapping and aerial hunting operations between July 3 and November 22, 2005. Seventy-seven field necropsies were performed, and 256 blood samples were conveniently collected during the eradication process. As part of the eradication strategy, the island was arbitrarily fenced into five zones based primarily upon fencing convenience (Fig. 1). True random sampling was not possible due to logistical constraints, but all pigs dispatched during the sample periods were bled for serology. Since porcine blood is prone to rapid hemolysis, rendering the samples unfit for some serologic analyses, we made efforts to draw blood from carcasses in the field within five minutes of dispatch. Global Positioning System (GPS) locations of the pigs were recorded by the hunters and plotted in a random subset, 241/256 (94%), of pigs sampled (Fig. 1). This subset of sample locations represented a variety of habitats, including grassland (52%), coastal sage brush (17%), shrubland (13%), chaparral (6%), oak woodland (4%), fennel (4%), human land use (3%), and riparian (1%). Barren and forest habitats were not represented. Sage and chaparral habitats were particularly

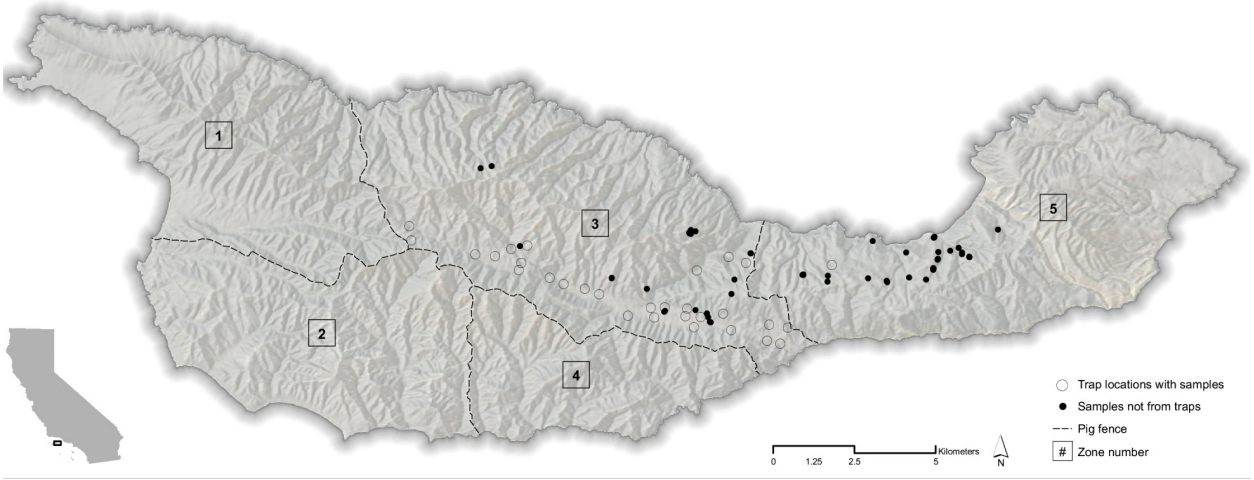

Figure 1. Santa Cruz Island showing numbered hunting zones, and locations of where pig carcasses for sampling were collected.

underrepresented in the study, and grasslands and scrublands were highly overrepresented, likely due to ease of targeting and trap setting in those areas. Sampling was convenience-based, since field visits were coordinated with times of early trappings in each region and most traps were set at sites with road access and where a higher density of pigs was expected. Pigs from non-trap locations (10% of total) were also sampled during each field period. The disparity between the age and sex of individuals sampled for serology, compared with a larger island-wide population subset, was 49% juveniles (84/172), and 51% adults (88/172), versus 68% juveniles (519/761) and 32% adults (242/761) (χ^2_1=22.15, p<0.001); 40% sows (84/211) and 60% boars (127/211), versus 36% sows (1288/3531) and 64% boars (2243/3531) (χ^2_1=0.81, p=0.37).

Age was estimated by visual examination of tooth eruption patterns and individuals were assigned to one of five age classes according to the classification protocol of Matschke (1967): I (<1 week to 6 weeks), II (7–19 weeks), III (20–51 weeks), IV (12–21 months), and V (>21 months).

Field necropsy examination was performed by either a pathologist or a practicing veterinarian (HK, KB) on 77 swine. Tissues of palatine tonsil, mandibular lymph node, lung, spleen, liver, brain, heart, thymus, diaphragm, small intestine, spiral colon, caecum, and kidney were collected in 10% buffered formalin (pH 7.2) for histopathologic evaluation. Paired tissues of palatine tonsil, mandibular lymph node, lung, spleen, liver, and brain were collected in separate sterile bags and stored frozen. Additional tissues from animals exhibiting gross lesions were collected when indicated. The small intestine, spiral colon, and caecum were examined for parasites and 5 g of contents from each were pooled and preserved in 10% formalin. A random subset of 54 of these pigs was examined for the presence of ectoparasites with an emphasis on a variety of organisms rather than quantitative numbers. Parasites were collected, preserved in 10% formalin, and shipped to the University of Tennessee for evaluation (SP).

Formalin fixed tissues were shipped to California Animal Health and Food Safety Laboratory (CAHFS), San Bernardino Branch, for histologic evaluation. Samples were processed by standard techniques, and tissues were sectioned at 4µm thick and stained with hematoxylin and eosin and examined microscopically (HK). In an individual with diseased tissues, lesions were described and then catalogued by organ affected, i.e., hepatitis would count as one "lesion," nephritis as a separate lesion, and pneumonia as a third. Causative agents such as parasites were only cited if visualized, or if inferred by the pattern of pathologic findings. Due to the incidence of pneumonia detected, a random subset of five individuals with interstitial pneumonia was screened for porcine circovirus using immunoperoxidase (IPX) histochemistry technique (HK).

Blood was drawn from the heart or chest cavity with focus on obtaining samples within five minutes of dispatch. We evaluated 240 samples for *Brucella* and *PRV* and 223 for *Leptospira* antibodies at CAHFS. Antibody specific to PRV was evaluated using a commercially available latex agglutination assay developed for domestic swine[1] (Schoenbaum et al. 1990). Buffered acidified plate agglutination (BAPA) was used to screen for antibody to *Brucella spp*. using *B. abortus* antigen supplied by the United States Department of Agriculture (USDA) National Veterinary Service Laboratory (NVSL) according to the procedure described in Uniform Methods and Requirements (UM&R). The screening assay, though designed to detect *B. abortus* exposure, is known to be antigenically cross-reactive with *Brucella suis* (Nielsen et al. 1999); therefore negative tests for *B. abortus* likely rules out *B. suis* as well (S. Hietala, personal communication 2007). A standard microagglutination test (microAT) was used to screen for six *Leptospira* serovars, including *L. interrogans* serovar Pomona, *L.i.* serovar Bratislava, *L.b.* serovar Hardjo, *L.i.* serovar Grippotyphosa, *L.i.* serovar Icterohemorragiae, and *L.i.* serovar Canicola. The microagglutination assay was performed using serial twofold dilutions of serum starting at a 1:100 dilution (Cole et al. 1973). Reference antigen and serovar-specific control antisera were supplied by the USDA NVSL. Positive serologic reactions were interpreted as evidence of exposure to disease rather than confirmation of active infection in the wild pig sampled.

We analyzed 256 serum samples for *Toxoplasma gondii* antibodies by the modified agglutination test (MAT) using formalin fixed tachyzoites as antigen (bioMerieux Laboratories, Lyon, France) at the University of Tennessee, College of Veterinary Medicine (UTCVM). Titers of 1:32 or greater were considered positive. Serum samples were analyzed for *Trichinella spiralis* antibodies (SafePath Laboratories ELISA), using microwells coated with *T. spiralis* excretory-secretory antigen. Samples with absorbance of 0.3 optical density units or higher were considered positive (SP). Serum was not analyzed for exposure to the introduced CSF (hog cholera) or any other "federally reportable" disease because we could not gain permission from U.S. Department of Agriculture Animal and Plant Health Inspection Service to test for these diseases.

Preserved external parasites and fecal samples were shipped to the UTCVM for evaluation. External parasites were examined microscopically for identification. A random subset of 69 fecal samples was collected from the 77 necropsies. Five grams of fecal material was taken from each of the small intestine, large intestine, and caecum and then combined into single specimens. Fecal samples were concentrated using centrifugal sugar flotation (Sheather's sugar solution specific gravity 1.275) and formalin-ethyl acetate sedimentation, and then examined microscopically (SP).

Comparisons between sexes and juveniles and adults were evaluated using Chi-Square for a 2X2 contingency table with a Yates correction for continuity. We also report 95% confidence intervals (95% CI) for the true prevalence of all pathologies within the population based on sample prevalence.

RESULTS

The sampling fraction of the total wild swine population of SCI tested for PRV and *Brucella* was 5% (240/5048); for *Toxoplasma* and *Trichinella* it was 5% (256/5048); and for the six serovars of *Leptospira* it was 4% (223/5048). Eighty-five percent of all sera and 90% of the carcasses were from Zone III; whereas 15% of the sera and 10% of the carcasses were from Zone V (Fig. 1). The sex ratio of the 211 sampled swine was 127/84 (boars/sows). Of these, the age class V adults had the largest sex disparity (48/19). This sex ratio is slightly more skewed than the larger island-wide sample of age class V pigs (105/53) (S. Morrison, personal communication 2007).

No antibody titers were detected for *Brucella*, PRV, *Toxoplasma* or *Trichinella*. While it is not possible to calculate 95% confidence intervals for these null results, the upper limit of the 95% confidence interval (assuming a single positive result) suggests that these diseases have a true prevalence of <2.2% in this population.

The overall apparent seroprevalence for *Leptospira* (all serovars) was 14.3% (32/223) (95% CI: 10.6%–18.8%), with 31% (10/32) showing titers

1. Viral Antigens, Meridian Life Sciences, Memphis, TN (http://www.meridianlifescience.com).

Table 1. Apparent seroprevalence of *Leptospira spp*. in feral pigs (*Sus scrofa*) sampled in 2005 from Santa Cruz Island, California.

Leptospira serovar	N	≥1:100	Seroprevalence (%)	95% CI	Std. error
L.i. Canicola	223	3	1.3	0.4–3.4	8.1
L.i. Grippo	223	16	7.2	4.6–10.7	6.4
L.i. Hargjo	223	0	0	ND*	-
L.i. Ictero	223	15	6.7	4.2–10.2	6.5
L.i. Pomona	223	2	0.9	0.2–2.8	9.4
L.i. Bratislava	223	12	5.4	3.1–8.6	6.6
Total # tested**	223	32	14.4	10.6–18.8	6.8

≥1:100 dilution titer denotes exposure to one or more *Leptospira* serovars.

*ND – No antibody detected at 1:100.

** Some individuals were positive to one or more serovars

(microAT) 1:100 to one or more serovars of *Leptospira* (Table 1). These low-level titers were considered to be indicative of past exposure rather than evidence of active infections. The seroprevalence of exposure to *Leptospira spp.* relative to sex was 14% (18/127) (95% CI: 9.3%–20.3%) boars and 16% (13/84) (95% CI: 9.4%–23.5%) sows, with one positive sample from an animal of undetermined sex. With respect to age class, the seroprevalence of exposure to *Leptospira* was 17% (14/84) (95% CI: 10.4%–24.8%) juveniles (age class I–III) and 16% (14/88) (95% CI: 9.9%–23.7%) adults (age class IV and V). Samples were positive from four pigs of undetermined age. There was no significant difference in prevalence of *Leptospira* between boars and sows, or between juveniles and adults (χ^2_1<0.01, p>0.99 for both comparisons).

Gross examination was performed on 77 carcasses consisting of 65% (50/77) boars, 32% (25/77) sows, and 3% (2/77) undetermined sex. No gross lesions indicative of population-level disease were noted in any of the animals examined. Sixty-two percent (48/77) (95% CI: 52.4%–71.6%) of the pigs had mild, non-specific microscopic lesions in one or more organs (Table 2). Interstitial pneumonia characterized by mild multifocal lymphocytic infiltrates was seen in 38% (29/77) of the necropsied animals. The distribution of combined lesions among the different groups was 76% (19/25) in sows and 58% (29/50) in boars. The 77 pigs showed various non-specific incidental lesions in different organs. Among the 63 aged individuals, there was no significant difference (χ^2_1=2.19, p = 0.14) in numbers of juveniles (I–III) (83%, 15/18) (95% CI: 62.3%–95.3%) with pathology as compared to adults (IV–V) (60%, 27/45) (95% CI: 46.7%–72.3%). There was, however, a marginally significant number of pigs with lesions in age class V (19/34=56%) (95% CI: 9.9%–23.7%) compared

Table 2. Histopathological findings for Santa Cruz Island feral pigs (*Sus scrofa*) in 2005 from Santa Cruz Island, California.

Histopathology findings (N=77)	Number of findings	Incidence
Interstitial pneumonia	29	38%
Pulmonary hemorrhage	2	3%
Interstitial nephritis	1	1%
Hepatitis	1	1%
Myositis	4	5%
Sarcocyst	7	9%
Eosinophilic enteritis*	4	5%
Tonsilitis	18	23%
Cervical lymphadenopathy	5	7%
Chronic abscess	3	1%
Total # pigs with lesion	48†	62%

* Possibly due to parasitic migration.

† Individuals may have ≥1 pathological findings.

to juveniles (χ^2_1=2.80, p=0.094). Thirty-eight percent (29/77) (95% CI: 28.4%–47.6%) of the animals had no remarkable lesions in any of the tissues examined. Although pathologic changes were seen in the liver of one pig and interstitial nephritis of the kidney of another, none of the pigs with positive titers for *Leptospira* showed pathology in the commonly affected organs. Overall, there were no remarkable lesions noted in the swine population to suggest an active population-disease process.

Fecal sample concentration yielded: eggs of *Metastrongylus spp.* (lungworm) in 9% (6/69) (95% CI: 3.9%–16.4%); *Demodex sp.* ("mange" mite) in one fecal sample (95% CI 0.1%–7.7%); *Eimeria sp.* oocysts 3% (2/69) (95% CI: 1.2%–10.9%) and grain mites or their eggs in 17% (12/69) (95% CI: 10.4%–26.6%) of the samples. A few of the samples contained unidentified coccidian oocysts that were not compatible with *Eimeria* or *Isospora* species typical of swine. Twenty percent (14/69) (95% CI: 12.7%–29.9%) contained grain mites or parasite eggs that were considered to be non-specific to swine. External parasites identified on pigs examined included *Haematopinus suis* (hog louse) 80% (43/54) (95% CI: 68.5%–88.1%); *Pulex irritans* 13% (7/54) (95% CI: 6.2%–23.0%); and *Ixodes pacificus* 6% (3/54) (95% CI: 1.5%–13.7%). *H. suis* was detected commonly during all visits, *P. irritans* was seen once in July and the remainder in October and November, and *I. pacificus* was found in October and November only.

DISCUSSION

In spite of the background pathology present and evidence of exposure to several serovars of *Leptospira*, data suggest that the subset of SCI wild pigs examined was from a generally healthy population with no detectable ongoing population-disease processes. However, since several serovars of *Leptospira* were unexpectedly found in an atypical host, it raises questions as to the potential of cross-infection to an island native as a naïve accidental host.

Methodology and Data Biases

The serum sampling had a convenience-based bias, as the majority of traps were set primarily in open areas along roads and in the long central valley that courses longitudinally through the island. Trap-wary pigs would be less likely to be represented. It may be assumed that the subset of pigs along roads would be more likely to interact, due to more convenient travel access, as opposed to some smaller subpopulations that may have been more isolated by geographic barriers. This would likely bias the data to reflect a higher incidence of disease than the total population prevalence.

Contrary to the age ratio observed in the island-wide survey, significantly fewer juveniles than adults were represented in this study (p 0.001). The reason for this discrepancy was undetermined. Nevertheless, adults, having lived longer than juveniles, could have greater opportunities for exposure to diseases endemic to the island. The selection of older individuals, with the expected increased probability of disease exposure over time, and those with external lesions or in poor condition, could potentially bias the necropsy results toward a higher incidence of pathology. However, the data show a marginally greater number of pigs with lesions in juveniles than in adults (age class V). This may be due to some acquired-immunity effect in adults, which may protect surviving individuals (Lankester 2001, 239; Fallon et al. 2003). Although a 30% rate of interstitial pneumonia in the population may appear high, it was comparable to pig farms where a moderate prevalence is considered to be in the range of 30%–70% (Pointon et al. 1984; Radostits et al. 2000). In our opinion, the gross and histologic pathology findings in this pig population represented mild, incidental, non-specific background lesions without evidence of an active population-disease process.

Because of the hemolytic nature of porcine blood there was hemoglobin contamination in some serum samples. Some of the laboratory analyses, particularly the *Leptospira* titers, were more sensitive to hemoglobin contamination. The respective laboratories discarded contaminated samples as invalid for each method; hence, the discrepancy in sample size between the different serologic tests. The serologic assays used in this study were developed for use in domestic species and are not data to reference diagnostic sensitivity and specificity for feral pigs. With most serological testing performed on wildlife species there is a general assumption that individual assays will

detect antibodies with similar performance as was documented for domestic species (Hietala and Gardner 1999). These are considered screening assays with high detection sensitivity, but include the possibility of false positive results due to antigenic cross-reactivity with other organisms sharing similar surface antigens. The BAPA test for *Brucella* is the standard used for herd screening in domestic swine since it has up to 100% sensitivity (Barton 1996; Olsen et al. 1996), although a wide range of specificity values are reported. Since all pigs tested negative for *Brucella*, the specificity of this test is inconsequential. The pseudorabies assay specificity is approximately 95%, also as measured for domestic swine. In the microAT test for *Leptospira*, as in other agglutination assays, serologic cross-reaction is known to occur, and extremely elevated titers are more likely to show cross-reaction to related surface antigens. The tested serotypes do have some shared surface antigens, so cross-reactivity is expected between *L.i.* Bratislava and *L.i.* Pomona, as well as a lower level cross-reactivity between *L.i.* Icterohemmorhagiae and *L.i.* Pomona. For example, a high antibody titer of *L.i.* Bratislava of >1:3200 can cause a low reaction (such as 1:100) in *L.i.* Pomona, or a >1:3200. *L.i.* Pomona can pull up an *L.i.* Bratislava to 1:100. The highest serologic response generally indicates the serovar to which it is exposed, and the higher the titer in one serovar the more likely it is to cross-react and artificially raise the titer in the other serovar. The titers for *Leptospira* measured in this study did not exceed 1:200. This decreases the chances of cross-reaction (S. Hietala, personal communication 2007). There are no published evaluations of *Leptospira* serology performance for swine. In assessments of MAT for other species, however, the sensitivity was low (30%) in early acute-phase cases and increased to 76% in convalescence, while specificity was less than or equal to 97% (Cumberland et al. 1999). Therefore, while the prevalence of *Leptospira* may be underestimated by this technique, the probability of false positives is low.

In those necropsies done by a practicing veterinarian, rather than the pathologist, subtle lesions may have been overlooked, thereby underestimating prevalence of pathologic changes. The lack of population disease seen on gross and microscopic examination is noteworthy in light of the fact that the subset was a purposely biased selection of an older, and therefore more likely exposed, population sample.

Implications

Our objective was to document whether there were diseases in SCI pigs that would have zoonotic implications or be of conservation interest to native fauna on or around SCI, including marine mammals and the SCI fox.

Sarcocystis found in heart and skeletal muscles of pigs are incidental findings and are of no clinical relevance. The grain mites and the unidentified coccidian oocysts, that were non-specific to swine and were detected in fecal samples, were presumably ingested from an exogenous source. Since grain mites and their eggs were fairly abundant, it is likely they were consumed with the corn that was used for baiting the pig traps. The unidentified coccidian oocysts were likely passed from ingested prey. The *Pulex irritans* and *I. pacificus* found on the pigs may also have been "host-sharing" with the SCI fox and spotted skunk (Crooks et al. 2001; Crooks et al. 2004). The lone *Demodex sp.* mite recovered in a fecal sample is the first documented on SCI. This finding should be considered in the differential diagnosis of chronic skin lesions in the captive island foxes, should they reoccur.

There was no significant difference between juveniles and adults in the prevalence of detectable antibody titers for any of the diseases. For PRV, this is in contrast to prevalence findings in studies of pigs on SCaI (Timm et al. 2005), in Georgia (Pirtle et al. 1989), and in Florida (Van der Leek et al. 1993), where the probability of exposure appeared to increase with age. It had been hypothesized this disparity was due to maternal-sibling grouping of young pigs, thereby reducing exposure. However, recent work by Romero et al. (2001) has shown that transmission of the PRV strain indigenous to feral pigs is preferentially by venereal route, suggesting that exposure is primarily in adults.

Transmission of *Leptospira* is primarily from urine and contaminated water sources (Gummow et al. 1999). After weaning, exposure would be similar in all sex and age groups using a water source, regardless of the size of their home range. There was no significant difference in titers between sexes for

any of the diseases tested, which agrees with the findings of the above authors for PRV.

The most important finding of this study relative to SCI fox conservation was the lack of evidence of exposure of SCI pigs to PRV during the feral pig eradication. This is in contrast with the PRV seroprevalence of 25% in the SCaI pig population (Timm et al. 2005). PRV infection is acute and has a high mortality in experimentally infected foxes (Quiroga et al. 1995) and in most non-porcine secondary hosts in the wild (Thawley and Wright 1982; Weigel et al. 1996; E. Hahn, personal communication 2007). Although there is no evidence implicating PRV in the fox population decline on SCaI, finding PRV antibodies in the SCaI pig population and having a concurrent decline in fox or other wildlife populations during the pig eradication (Timm et al. 2000), where infected pig carcasses are available for scavenging, raises interesting questions regarding potential exposure of wildlife. Further data, such as testing of fox tissues for evidence of exposure to PRV, would be needed to address these questions. Since these coincident circumstances did not exist on SCI, decline of the SCI fox population due to PRV exposure is very unlikely.

The lack of evidence of *Brucella* infection supports the results of previous testing of 61 individuals in the SCI swine population (Corn 1987b) that were also negative (Corn 1987c). This is significant to the hunters participating in the eradication efforts to have low risk of zoonotic transmission of brucellosis.

Although there are no cats on SCI, the finding by Garcelon et al.(1992) of low-level seroprevalence for *Toxoplasma gondii* in SCI foxes may not necessarily be false positive laboratory results, as hypothesized, since the findings were repeated in the recent study (Clifford et al. 2006). However, data suggest that it is unlikely that transmission to foxes by eating wild pig carrion was a contributing factor. *T. gondii* infection could be sustained in the population by SCI foxes scavenging carcasses of marine mammals or eating fresh meat of birds. It is interesting to note that the single fox carcass recovered during the rapid decline of SCaI foxes had evidence of infection of *T. gondii* and the importance of the co-infection is unknown (L. Munson, personal communication 2007).

Unlike SCaI, where *Trichinella* were found in muscle of pigs (Timm et al. 2005), no evidence of *Trichinella* was found in the SCI pig population either by serology, gross examination of muscle tissue, or by microscopic examination of diaphragm tissue for nurse cells. It is doubtful the SCI pig population was a reservoir for infection on the island. There have been suggestions, however, of potential low level cannibalism in foxes in Italy (Rémonti et al. 2005) which could perpetuate transmission of *Trichinella* infection within a fox population without an intermediate host. Regardless of this potential, *Trichinella* infection within a fox population would not represent a conservation threat.

The spectrum of titers for different serovars of *Leptospira* is interesting in light of the variety and history of mammalian inhabitants on SCI over the last 20 years. The current four indigenous land mammals, the past four ranching mammals (including dogs), and marine mammals which "haul-out" or wash up as carcasses on the beaches, as well as the eight recorded bat species (Brown 1980) need to be considered in the epidemiology of *Leptospira.* The expected prevalence of *Leptospira* in a wild swine population is estimated at 5% (E. Bush, personal communication 2008). This data suggests that SCI wild swine were exposed to a number of serovars of *Leptospira*.

L. i. Grippotyphosa represents the highest titers of any serovar tested (7%), although there have been no reports of raccoons on SCI. This serovar has been shown experimentally to pass to wild carnivores when fed infected rodents (Reilly 1970), however, recent work has revealed no evidence of antibodies to this serovar in the SCI fox (Clifford et al. 2006).

Although they are the primary host of *L.i.* Icterohaemorrhagiae, there have been no confirmed sightings of rats on SCI. Incidental hosts include mice, skunk, fox, and bat (Clark et al. 1961; Ward et al. 2004; Matthias et al. 2005). Our 6% prevalence rate is not unexpected in light of the fact that Garcelon et al. (1992) reported a prevalence of 14% in the SCI foxes. SCI was the only one of six Channel Islands with foxes to have any evidence of *Leptospira* exposure for the two serovars tested in that study. No antibody titer to *L.i.* Icterohaemorrhagiae was detected in the SCI fox survey in 2001–2003 (Clifford et al. 2006) or SCI spotted skunks in 2000–2001 (Bakker et al. 2006). It

is interesting that by the 2001–2003 survey of the SCI fox, there was no evidence of this serovar in the sample tested.

Leptospira i. Bratislava displayed a 5% antibody response in the study population and is reportedly indigenous in feral pigs (Corn et al. 1986). Serologic studies in the United States and Canada indicate that Bratislava has become the serovar that most frequently affects swine (Bolin and Cassells 1992). It is noteworthy that 7% (2/28) of the wild SCI fox population showed evidence of exposure to this serovar (Clifford et al. 2006), but the captive-born SCI fox showed no evidence of exposure. This finding suggests that there was exposure of fox in the wild from the pigs or other mammals. The SCI spotted skunk has not been tested for this serovar. This serovar has been reported in rodents and dogs and it is considered they could serve as carriers; however, Moore et al. (2006) cite dogs as an incidental host for this serovar.

Leptospira i. Canicola only produced a positive antibody response in 1% of the study population. The presence of *L.i.* Canicola exposure is interesting since the dog is considered to be the primary reservoir host (Ward et al. 2004; S. Hietala, personal communication 2007). Over the past 20 years, with the exception of pig-hunting dogs, dogs have been typically limited to the main ranch area and/or incidental illegal entry to the shore for short periods from oceancraft. No antibodies to *L.i.* Canicola were reported in the 29 SCI foxes tested by Garcelon et al. (1992), nor by Clifford in 2001–2003, nor in 28 SCI spotted skunks tested in 2000–2001 (Bakker et al. 2006).

Leptospira i. Pomona titer levels were also relatively low (1%) in the study population. *L.i.* Pomona has been shown to have a markedly pathogenic effect on California sea lions (*Zalophus californianus*) and appears to be responsible for periodic die-offs along the mainland. There has been suggestion that a source of contamination may be small mammals or pigs living on the Channel Islands (Gulland et al. 1996). No evidence of exposure to this serovar was found during testing of 28 SCI spotted skunks in 2000–2001 (Bakker et al. 2006) and 28 SCI foxes in 2001–2003 (Clifford et al. 2006). These data from SCI pigs suggest that pigs were not a primary source of *L.i.* Pomona to sea lions.

Although data indicate exposure of the SCI pigs to several serovars of *Leptospira*, there has been no report of pathology attributed to Leptospirosis from the necropsies done on the SCI fox population to date (L. Munson, personal communication 2008). The overall conservation threat to the SCI fox from Leptospirosis appears to be low at this time. Because of the behavior of *Leptospira* organisms, the ecology of *Leptospira* in island natives bears monitoring of a variety of serovars, particularly in a threatened or endangered population.

CONCLUSIONS AND RECOMMENDATIONS

Although there were parasites and background pathology present and there was evidence of exposure to several serovars of *Leptospira* in this sample of SCI wild pigs, this was generally a healthy sub-population with no detectable ongoing population-disease processes. There is no evidence that the wild pigs or the eradication efforts on SCI posed a zoonotic threat to hunters nor a conservation threat to the SCI fox or other island species. These studies underscore the importance of pathogen screening on a species prior to eradication to preserve data and to aid preventative management of sylvatic and zoonotic transmission during the efforts.

These studies and findings supplement other works showing the complexity of interactions between different serovar of *Leptospira* with primary and alternative hosts. It is not likely that Leptospirosis will become a major conservation threat on SCI; however any serovar now documented on the island could potentially become virulent if the un-adapted serovar infected a new host species. With an endangered insular native mammal population on SCI, more effort devoted to land and sea mammal serologic surveillance may be desired to address potential reservoirs, particularly for *Leptospira* and *T. gondii,* in order to anticipate potential sylvatic interactions in the island ecosystem.

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