SMALL MAMMAL POPULATIONS IN POST-FIRE BLACK SPRUCE (*Picea mariana*) SERAL COMMUNITIES IN THE UPPER KOBUK RIVER VALLEY, ALASKA.

Gates of the Arctic National Park and Preserve

Shelli A. Swanson

Technical Report NPS/AFARBR/NRTR-96/30

United States Department of the Interior • National Park Service • Alaska Region

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Abstract: Small mammal species distribution and abundance were examined through removal trapping in 4 post-fire seral stands of black spruce (*Picea mariana*) in the upper Kobuk River Valley, Brooks Range, Alaska, 1992-1994. Grids were positioned on burned and mature lichen woodland and burned and mature moss/shrub forest habitat pairs. Seven species of small mammals were captured. Red-backed voles (*Clethrionomys rutilus*) were most abundant and widely distributed. Yellow-cheeked voles (*Microtus xanthognathus*) were closely tied to areas with good burrowing conditions and adequate supplies of rhizome-producing plants (primarily early seral invaders) and graminoids. Masked shrews (*Sorex cinereus*) were the most abundant of the 3 shrew species captured. Snap traps accounted for 59% of the small mammal captures, but lemmings (*Synaptomys borealis* and *Lemmus trimucronatus*) and shrews were captured only in pitfall traps. Species diversity and abundance were highest in the burned moss/shrub forest habitat and lowest on unburned lichen woodland habitat. Both burned habitats had higher species diversity and abundance than their corresponding mature component. Species diversity was similar on the two burned habitats and also on the two mature habitat types, but small mammal biomass was significantly higher on the moss/shrub lichen grids than on the lichen woodland grids. Small mammal habitat use and diversity appear to be related to: 1) moss and organic mat depth; 2) berry production and availability; 3) abundance of early seral stage plant species and graminoids for food; 4) herbaceous layer development and substrate relief for cover requirements; and 5) moisture/humidity level in the soils and organic mat. A marked decline in small mammal populations was observed in all 4 habitat types in 1994 and was accompanied by increased litter size in red-backed voles, decreased species diversity, and low marten (*Martes americana*) harvest region-wide in the 1994-95 trapping season.

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INTRODUCTION

Since 1991, the National Park Service (NPS) has been collecting natural resource information from the Kobuk Preserve Unit of Gates of the Arctic National Park and Preserve. This information will enable NPS staff to make knowledgeable management decisions regarding potential road development across the Kobuk Preserve Unit to the Ambler Mining District (as authorized by section 201 of the 1980 Alaska National Interest Lands Conservation Act). Voles, shrews, and lemmings are integral components of the taiga ecosystem, such as that in the upper Kobuk River Valley. This study was initiated to obtain information on small mammal populations in the Kobuk Preserve Unit.

Dramatic population fluctuations are common in small mammals, and these fluctuations have exhibited a regular cyclicity north of 60° latitude in Europe (Hannson 1989, Hanski et al. 1991, Hanski and Korpimaki 1995). The causes of cyclic population fluctuations are not clear, but proposed factors include weather conditions, overwinter survival of juveniles and adult females, predation, food availability, length of breeding season, anti-herbivory compound development in plants, disease, and psychological stress at high population densities (Whitney 1977, West 1982, Krebs and Wingate 1985, Hansson 1989, Batzli 1992, Seldal et al. 1994). The reduced individual fitness and consequent high mortality found in high-density populations may also cause high density years to be followed by low density years (Buckner 1966, Fuller 1977).

Vole populations are the main food of ermine (*Mustela erminea*), least weasels (*M. nivalis*), and marten (*Martes americana*) (Strickland and Douglas 1987, King 1989, Nowak 1991, Martin 1994); consequently, changes in small mammal abundance greatly affect the population dynamics and abundance of these predators. A strong correlation between vole density and weasel density has been documented (Raymond and Bergeron 1982, King 1989), and though female ermine reproduce regardless of prey population density, the survival of young during the first year is directly dependent on immediate prey (vole) availability (Raymond and Bergeron 1982). A direct relationship between small mammal density and marten density has also been documented, and when small mammals are scarce, so are marten (Weckwerth and Hawley 1962, Thompson and Colgan 1987). Low microtine availability causes poor physical condition for female marten, lowered reproductive rates, increased juvenile dispersal, and larger home range sizes (Lensink et al. 1955, Weckwerth and Hawley 1962, Thompson and Colgan 1987).

Owls, hawks and other raptors are also affected by small mammal population cycling (Ehrlich et al. 1988). A direct relationship between vole density and short-eared owl (*Asio flammeus*) abundance was found by Clark (1975), and this relationship likely holds for other owl species. Nearly all northern owl species have been known to irrupt southward in response to low small mammal abundance (Ehrlich et al. 1988). Year-round owl residents of the Kobuk Preserve Unit include the northern hawk-owl (*Surnia ulula*), boreal owl (*Aegolius funereus*), great horned owl (*Bubo virginianus*), and great gray owl (*Strix nubulosa*), and all are known to periodically irrupt southward. During years of peak vole populations, raptor reproduction is greatly enhanced. The number of nesting pairs, mean clutch size, and number of hatchlings reared all increased in northern harrier (*Circus cyaneus*) populations in areas with high small mammal densities (Simmons et al. 1986); boreal owls, kestrels (*Falco sparvarius*), hawk owls, short-eared owls, and northern goshawks (*Accipiter gentilis*) also exhibit these trends (Bondrup-Nielsen 1978, Newton 1979, Korpimaki and Norrdahl 1991, Blem et al. 1993). Generalist raptors such as rough-legged hawks (*Buteo lagopus*) are able to switch to alternate prey during times of low vole density (Hanski et al. 1991) and are less affected by vole fluctuations.

In spite of the important role small mammals play in the taiga ecosystem, little information is available for small mammal species diversity and abundance in northern Alaska, particularly in the upper Kobuk River valley. Dean and Chesemore (1974) inventoried small mammal species at Walker Lake near the headwaters of the Kobuk River during their survey of birds and mammals in the Baird and Schwatka Mountains, and NPS conducted a preliminary small mammal survey along the Kobuk River in 1991 (Swanson 1991); small mammal abundance and population estimates were not obtained from these studies.

The goal of this study was to assess the status of small mammal populations in different post-fire seral stages in the Kobuk Preserve Unit and evaluate these populations as a prey base for furbearers and raptors. The following objectives were developed: 1) to determine small mammal species diversity and abundance in different-aged, post-fire black spruce stands in the Kobuk Preserve Unit; 2) to examine population dynamics for small mammal species through age, sex, weight, and reproductive information; and 3) to relate small mammal abundance, biomass, and population data to furbearer and raptor populations in the Kobuk Preserve Unit.

Funding for this project was provided by the Minerals Management Division, National Park Service, Anchorage Field Area Office. Fieldwork could not have been completed without the assistance of Ann Corson, Dave DeVoe, Donna DiFolco, Matt Irinaga, Tim Osborne, Mike Schnorr, and Kelly Shea. Dave Swanson [U.S. Department of Agriculture, Natural Resources Conservation Service (USDA-NRCS)] and Donna DiFolco collected soils and vegetation data. Editorial review was provided by Buddy Johnson (USFWS), Gordon Jarrell (University of Alaska Museum), Dave Swanson (USDA-NRCS), and Eric Rexstad (University of Alaska). This project is part of a cooperative study of small mammals in post-fire seral stages between Koyukuk/Nowitna National Wildlife Refuge, Kanuti National Wildlife Refuge, Gates of the Arctic National Park and Preserve, and University of Washington.

STUDY AREA

The study was conducted in the Kobuk Preserve Unit of Gates of the Arctic National Park and Preserve, Alaska (Fig. 1). The Kobuk River, a designated Wild and Scenic River, is located in Pleistocene glacial deposits along the southern foothills of the Brooks Range. Topography ranges from undulating plain in the valley bottom to high hills/low mountains forming the valley sides. Open, low-growing black spruce (*Picea mariana*) forest communities dominate the valley floor; black and white spruce (*P. glauca*) interspersed with occasional birch (*Betula papyrifera*) and aspen (*Populus tremuloides*) trees occur on the dry hilltops. In the westernmost part of the preserve, open moist tundra vegetation often separates tree communities. Willow (*Salix* spp.)/alder (*Alnus* spp.) thickets and tall white spruce and balsam poplar (*Populus balsamifera*) stands occur in the floodplain and along drainage areas.

Grid Site Descriptions

The burned lichen woodland grid (Fig. 2) was situated on an old stream terrace of coarse, loamy alluvium on top of gravel. Permafrost was not encountered in the soil pit, but water was located 72 cm below the organic layer. The organic layer was approximately 7 cm deep. Wildfire burned through the area in 1991 and vegetation was classified as black spruce dwarf tree scrub woodland (Viereck et al. 1992). Ground cover was composed of burned reindeer lichen (*Cladina rangiferina*), downed wood, and bare soil interspersed with unburned sphagnum moss (*Sphagnum* spp.) hummocks (Appendix I, Table IA). Live black spruce trees,

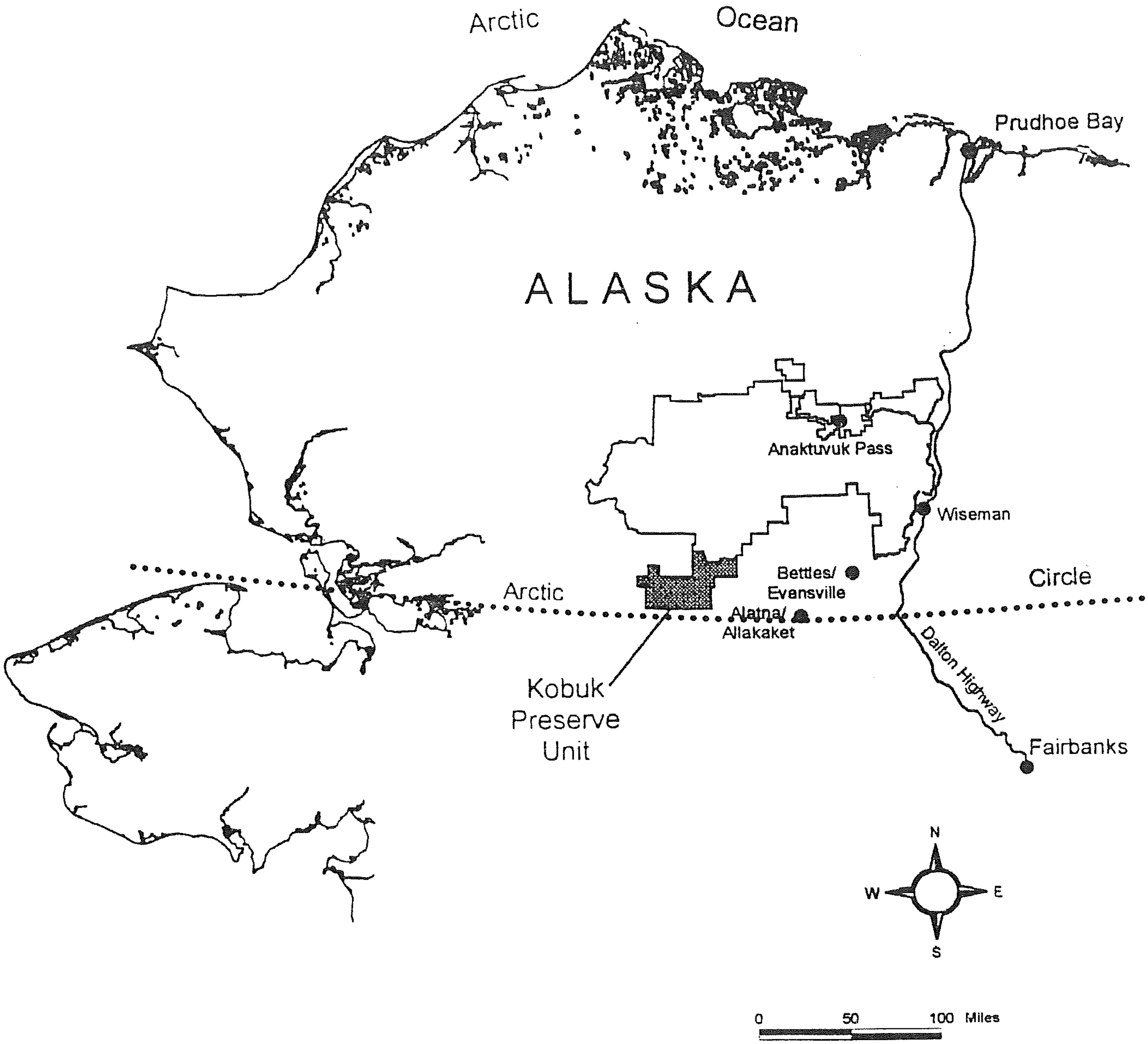

Fig. 1. Location of the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska.

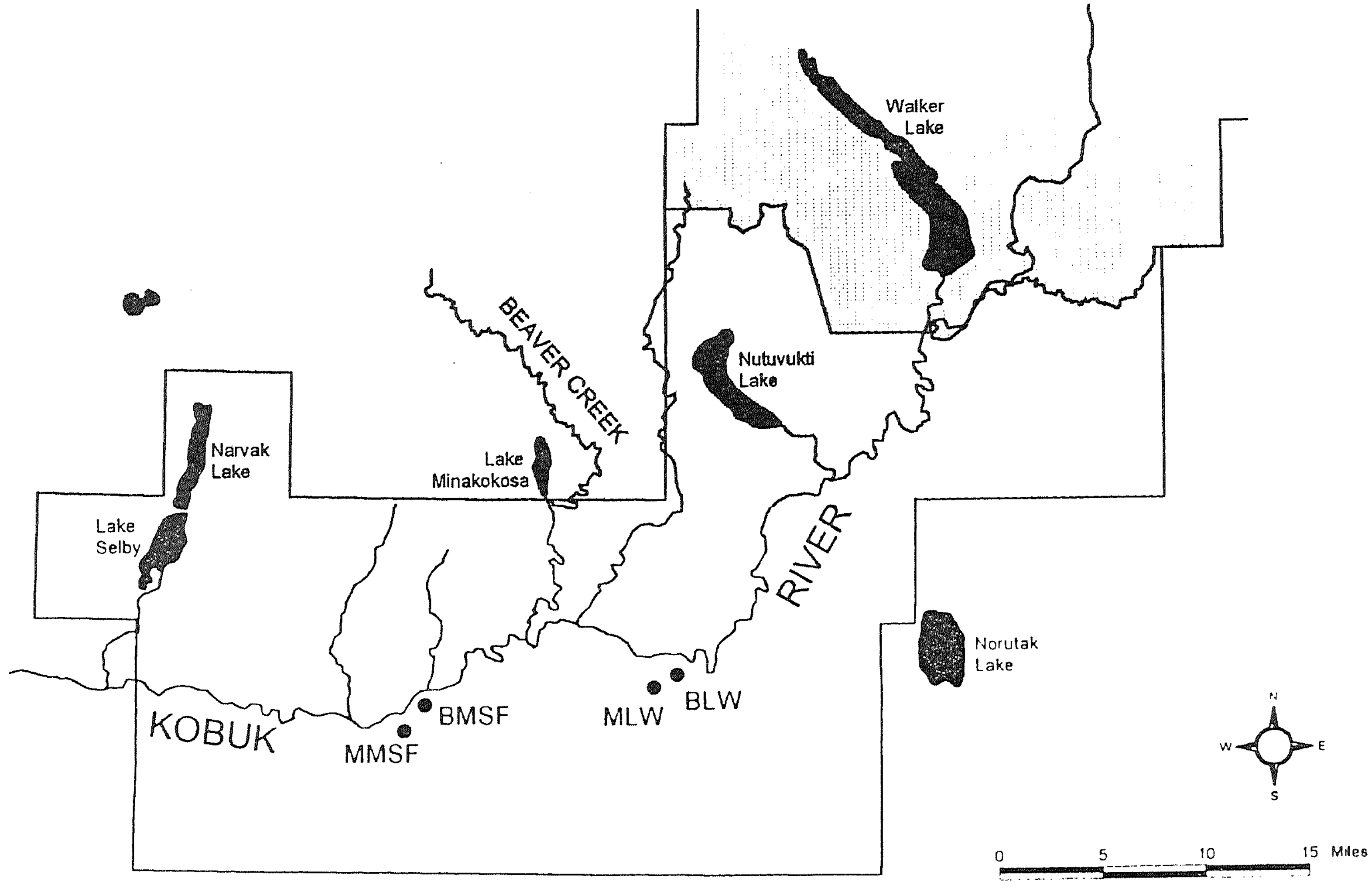

Fig. 2. Locations of small mammal trapping grids in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Alaska, 1992 - 1994. Grid codes are as follows: BLW - burned lichen woodland; MLW - mature lichen woodland; BMSF - burned moss/shrub forest; MMSF - mature moss/shrub forest.

0.5 – 8 m in height, accounted for approximately 33% of the standing tree stems and generally were found growing out of unburned sphagnum moss hummocks and other wet spots. Cloudberry (*Rubus chamaemorus*) and crowberry (*Empetrum nigrum*) were prominent on the grid but did not occur in the vegetation sampling plot.

The mature lichen woodland grid (Fig. 2) was located on a stream terrace of alluvium topped with 4 – 5 cm of organic material (D. Swanson, Nat. Resour. Conserv. Serv., unpubl. data). Permafrost was reached at 88 cm and 122 cm below the organic layer in the 2 soil pits. Vegetation was classified as black spruce woodland, a vegetation type which appears to be a fire climax stage (Viereck et al. 1992). The ground was covered by a dense lichen mat, composed predominantly of *Cladina rangiferina* and *C. stellaris* (Appendix I, Table IB). Black spruce trees within the grid were 6 – 8 m tall, with smaller seedlings underneath. There was little evidence of small mammal activity on the grid.

The burned moss/shrub forest grid (Fig. 2) was placed in a 16-year-old burn on a dissected loess-covered moraine area. Soils consisted of silty loess and permafrost was not encountered, probably having receded deeper into the soil after the fire. The organic layer was 9 cm deep at both soil pits dug near the grid. Mineral soils were compact and digging holes for the pitfall traps was difficult. Soils were biochemically reduced (indicative of wetness) below 30 cm at the eastern side of the grid and below 60 cm at the western side. Vegetation was classified as low mesic shrub birch-ericaceous shrub (Viereck et al. 1992), and probably was open black spruce forest prior to the burn. Ground cover consisted of mosses, bare soil, downed burned trees, and a few forbs (Appendix I, Table ID). Standing dead trees, 3 – 4 m in height, accounted for less than 5% of the ground cover. The shrub layer was the most highly-developed vegetation component on the site (Appendix I, Table ID), and blueberry (*Vaccinium uliginosum*) productivity was high. Evidence of small mammal digging, tunneling, and feeding activity was abundant.

The mature moss/shrub forest grid (Fig. 2) was situated on a ridge in the same landscape unit as the burned moss/shrub forest grid. An 18 to 21 cm organic mat covered mineral soil. Soils were saturated below 12 cm and, contrary to the burned moss/shrub forest grid, permafrost was encountered 55 cm below the organic mat. The southeast corner of the grid abutted a wet thermokarst depression with the water table at the surface. Vegetation was classified as open black spruce forest, commonly a climax stage on cold, poorly drained sites (Viereck et al. 1992). This vegetation type burns frequently and stands older than 100 years are rare (Viereck et al. 1992); there was no evidence of previous fire in this stand. Ground cover was predominantly moss/lichen with a shrub layer of blueberry, dwarf birch (*Betula glandulosa*), and Labrador tea (*Ledum palustre*) (Appendix I, Table IC). Multi-strata black spruce made up the remainder of the overstory. Small mammal runways, diggings, and feeding sites were numerous.

METHODS

Field Methods

Fieldwork was conducted in August to sample peak annual small mammal populations. Trap stations, consisting of 2 museum special snap traps (baited with peanut butter and oats) and a pitfall trap, were placed 10 m apart on 100 x 100 m trapping grids. Four grids were established (2 in 1992 and 2 more in 1993; Fig. 2) and operated for 900 trapnights per grid per year during the study. Trapnights were defined as 1 trap set for a 24-hour period.

Captured animals were identified to species, weighed, and aged as juvenile, subadult, or adult based on molt patterns and weight. Data on testes development and mammary and vulva condition was collected. Embryos and placental scars were counted when visible. Study skins and skeletons prepared during the study are housed at the University of Alaska Fairbanks (UAF) Museum. Kidney, heart, and liver tissues were collected for the UAF Museum's frozen tissue collection for future research on genetics and environmental pollutants.

Paired grids were located in mesic black spruce vegetation in two areas along the Kobuk River (Fig. 2); grids were located on the valley floor but were not on the floodplain. One grid pair was located in lichen woodland habitat, with one grid in a recently burned area and the other in nearby unburned mature vegetation. The second grid pair was established in moss/shrub forest habitat, with one grid in a 16-year-old burn and its complement in nearby in mature forest. Percent cover was estimated for all plants in a randomly selected 10 x 10 m plot within each grid (Appendix I). Vegetation communities were classified according to Viereck et al. (1992). Soil classification and stratigraphic information was collected from 2 soil pits at each grid site (D.K. Swanson, Soil Conserv. Serv., unpublished data) and is summarized under the STUDY AREA section above.

Statistical Methods

Population estimates were derived from small mammal trapping data using the program CAPTURE (Otis et al. 1978, White et al. 1982). The chi-square goodness of form test was used to assess model fit to the data collected (White et al. 1982). A z-test was used to compare population estimates between trapping grids and between years on the same trapping grid.

The Shannon-Weaver diversity index was used to assess species diversity for each trapping grid (Zar 1974). Species evenness (measuring the distribution of individuals among the species present) and species richness (the number of species captured) was also calculated. Differences between diversity indices were tested using a t-test (Hutcheson 1970, Zar 1974).

Relationships between the sex composition of captured small mammals (male:female) and the vegetation types they were captured in were examined by comparison with a binomial probability distribution. Associations between age ratios (immature:adult female) and vegetation types were examined using the chi-square test (Bailey 1981); for analytical purposes, juvenile and subadult categories were lumped to form an immature category. One-way analysis of variance was used to determine differences in the mean number of placental scars/embryos between years. Relationships between age and trap type were examined using the chi-square test. Bonferroni confidence intervals (Neu et al. 1974, Byers and Steinhorst 1984) were used to determine if differences between observed and expected values in chi-square contingency tables were statistically significant.

RESULTS

Species Distribution, Abundance, and Biomass

Red-backed voles, dusky shrews (*Sorex monticolus*), and masked shrews were captured at all 4 grid sites, and yellow-cheeked voles and northern bog lemmings (*Synaptomys borealis*) were found on 3 grid sites, both burn sites and the mature moss/shrub forest site (Tables 1 and 2).

Table 1. Numbers of small mammals captured on 100 x 100 m grids in burned lichen woodland (BLW) and mature lichen woodland (MLW) during 3-day trapping sessions in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992-1994.

Species	1992		1993		1994	
	BLW	MLW	BLW	MLW	BLW	MLW
Yellow-cheeked vole	9	0	4	0	6	0
Red-backed vole	5	3	7	7	0	0
Masked shrew	0	0	7	1	0	0
Dusky shrew	1	0	0	1	0	0
Northern bog lemming	1	0	0	0	0	0
Brown lemming	0	0	1	0	0	0
Total captures	16	3	19	9	6	0

Table 2. Numbers of small mammals captured on 100 x 100 m grids in burned moss/shrub forest (BMSF) and mature moss/shrub forest (MMSF) during 3-day trapping sessions in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1993-1994.

Species	1993		1994	
	BMSF	MMSF	BMSF	MMSF
Yellow-cheeked vole	37	10	9	0
Red-backed vole	59	53	12	14
Masked shrew	21	19	5	1
Pygmy shrew	3	0	3	2
Dusky shrew	1	1	0	0
Northern bog lemming	1	1	0	0
Total captures	122	84	29	17

Brown lemmings (*Lemmus trimucronatus*) were captured only on the burned lichen woodland grid. Three shrew species were found on the burned moss/shrub forest grid; pygmy shrews (*Sorex hoyi*) were captured only in this vegetation type (Table 2).

Of the 305 animals captured during the study, 53% were red-backed voles, 25% were yellow-cheeked voles, and 18% were masked shrews. Red-backed voles were the most abundant species on all grids except the burned lichen woodland grid (Tables 1 and 2). On the burned lichen woodland grid, more yellow-cheeked voles were captured than red-backed voles in 1992, and only yellow-cheeked voles were captured on this grid in 1994 (Table 1). The red-backed vole was the only species captured on the mature lichen woodland grid in 1992, and when animal abundance was low on all grids in 1994, even this species was absent. Shrews were most abundant in the mature moss/shrub forest and burned moss/shrub forest (Table 2).

Based on population estimates, small mammal abundance was highest on the burned moss/shrub forest grid and lowest on the mature lichen woodland grid (Table 3). Small mammal abundance on all grids was highest in 1993 and lowest in 1994. In 1994, so few animals were captured during fieldwork that an acceptable population estimate could only be obtained for the burned moss/shrub forest grid (Table 3). The population estimate for the burned moss/shrub forest grid was higher in 1993 than in 1994 ($Z = 1.78$, $\underline{P} = 0.075$). Higher small mammal population estimates were obtained on the moss/shrub forest grids than on the lichen woodland grids (Table 3).

Though more small mammals were captured on the burned lichen woodland grid than on the mature lichen woodland grid (Table 1), the population estimate did not differ between the two in 1993 when estimates were obtained for both grids ($Z = 0.84$, $\underline{P} = 0.401$; Table 3). In 1993, the population estimate for the burned moss/shrub forest was higher than that for the mature moss/shrub forest ($Z = 1.29$, $\underline{P} = 0.075$). Comparison of the burned grids in 1993 show small mammal abundance was higher on the burned moss/shrub forest than on the burned lichen woodland ($Z = 4.06$, $\underline{P} = 0.000$). In 1993, small mammal abundance was higher in the mature moss/shrub forest than on the mature lichen woodland ($Z = 4.21$, $\underline{P} = 0.000$).

Trends in small mammal biomass per hectare reflect population estimate trends (Tables 3 and 4). Small mammal biomass was highest on the burned moss/shrub forest grid and lowest on the mature lichen woodland grid (Table 4). Small mammal biomass dropped by 78% on the moss/shrub forest grids from 1993 to 1994 and by 32% on the burned lichen woodland site during the same time; no small mammals were taken from the mature lichen woodland grid in 1994.

On the 2 burn grids, yellow-cheeked voles accounted for 49 - 100% of the total biomass, while on the mature grids, yellow-cheeked voles were captured only in 1993 in the moss/shrub forest and they comprised 36% of the biomass (Fig. 3). When present, red-backed voles accounted for 59 - 100% of the small mammal biomass on the mature vegetation grids and 19 - 40% on the burned grids. Shrews and lemmings generally made up 5% of the biomass per grid, but in 1993 they accounted for 12% of the biomass in the burned lichen woodland. The percentage of biomass contributed by each species in the burned moss/shrub forest remained constant from 1993 to 1994, even though animal numbers declined significantly between those years (Fig. 3).

Table 3. Population estimates (N), standard errors (S.E.), approximate 95% confidence intervals (C.I.), capture probability (p), chi-square goodness of fit test statistics (X^2), X^2 probability values (P), and sample sizes (n) for small mammals captured on four 100 x 100 m grids in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 1992-1994.

Grid[1]	N[2]	S.E.	C.I.	p	X^2	P	n
1992							
BLW	21	8	16 - 62	0.335	1.85	0.173	16
MLW	*						3
1993							
BLW	28	13	20 - 90	0.306	1.01	0.315	19
MLW	12	6	9 - 45	0.355	1.14	0.285	9
BMSF	162	20	137 - 223	0.372	0.44	0.509	122
MMSF	113	18	93 - 171	0.364	0.45	0.502	84
1994							
BLW	*						
MLW	*						
BMSF	57	39	32 - 244	0.210	0.54	0.461	29
MMSF	19	3	17 - 33	0.515	6.50	0.011	17

[1]Grid vegetation codes are as follows: BLW--burned lichen woodland, MLW--mature lichen woodland, BMSF--burned moss/shrub forest, and MMSF--mature moss/shrub forest.

[2]Estimates were obtained from the computer program CAPTURE using a constant capture probability removal estimator (Otis et al. 1978, White et al. 1982).

* Model parameters could not be estimated since the number of animals captured did not diminish significantly between sampling occasions.

Table 4. Small mammal biomass estimates for four 100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992-1994.

Vegetation Type	Biomass (g/ha)[1]		
	1992	1993	1994
Burned lichen woodland	524	403	273
Mature lichen woodland	64	164	0
Burned moss/shrub forest		(3357)	(736)
Mature moss/shrub forest		(1623)	335

[1]Biomass is the combined weights of all small mammals captured per grid. Measurements in parentheses include weight estimates for animals marked and released alive from pitfall traps or those partially consumed while in the traps.

[2]The moss/shrub forest grids were trapped only in 1993 and 1994.

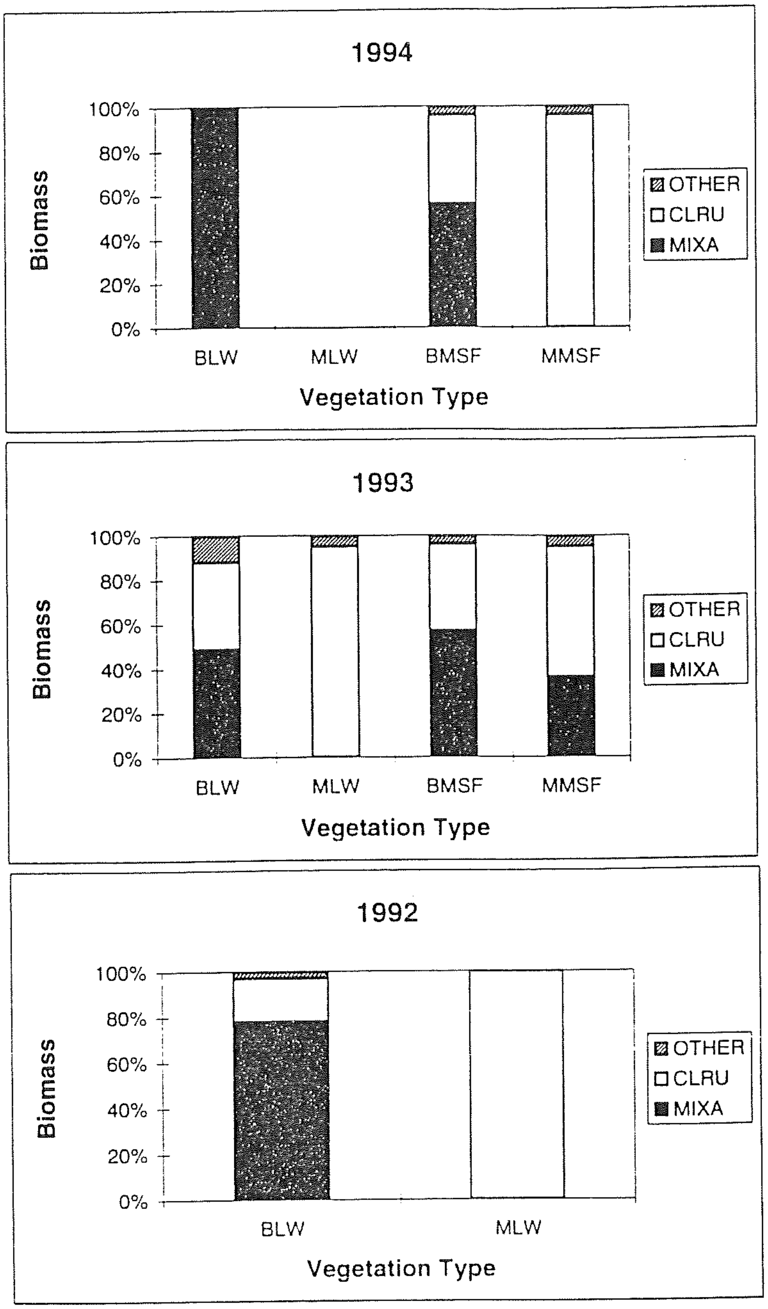

Fig. 3. Percent biomass of red-backed voles (*Clethrionomys rutilus*; CLRU), yellow-cheeked voles (*Microtus xanthognathus*; MIXA), and other small mammal species *(Sorex spp., Lemmus trimucronatus, Synaptomys borealis*; OTHER) captured on four 100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992-1994. Vegetation types are: BLW—burned lichen woodland, MLW—mature lichen woodland, BMSF—burned moss/shrub forest, and MMSF—mature moss/shrub forest.

Small Mammal Diversity

Overall, species diversity was highest in the burned lichen woodland and lowest in the mature lichen woodland (Table 5). Mature lichen woodland produced only 1 species in 1992, 3 species in 1993, and none in 1994 (Table 1). Six small mammal species were detected at both burn sites, but the burned lichen woodland had fewer captures and a more even distribution, resulting in a slightly higher diversity index (Table 5).

Species diversity indices were highest for all grids in 1993 when populations were high (Table 5). Species diversity in the mature moss/shrub forest declined slightly from 1993 to 1994 ($t = 1.77$, d.f. = 26, $\underline{P} = 0.088$), because the yellow-cheeked vole and northern bog lemming, both species captured on this grid in 1993, were not captured there in 1994 (Table 2). Higher species diversity was found on the mature lichen woodland in 1993 than in 1992 ($t = -2.51$, d.f. = 9, $\underline{P} = 0.033$); no animals were captured on this grid in 1994 (Table 1). Species diversity also declined in the burned lichen woodland from 1993 to 1994 ($t = 11.83$, d.f. = 19, $\underline{P} = 0.000$).

In 1993, when diversity indices were obtained for all 4 grids (Table 5), the burned lichen woodland was more diverse than the mature lichen woodland ($t = 1.83$, d.f. = 12, $\underline{P} = 0.092$). Species diversity on mature moss/shrub forest did not differ from that on the burned moss/shrub forest in 1993 ($t = -1.59$, d.f. = 161, $\underline{P} = 0.114$). However, in 1994, yellow-cheeked voles and pygmy shrews were collected from the burned moss/shrub forest but not from the mature moss/shrub forest (Table 2), giving the burned grid a higher diversity score ($t = -3.12$, d.f. = 30, $\underline{P} = 0.004$). In 1993, species diversity did not differ between the burned lichen woodland and the burned moss/shrub forest or between the mature lichen woodland and the mature moss/shrub forest grids ($\underline{P} > 0.30$); the small sample size for the mature lichen woodland (Table 3) probably biased the latter result.

Trends in 1993 were substantiated by comparisons of compiled data: the burned lichen woodland had higher small mammal species diversity than the mature lichen woodland ($\underline{P} = 0.020$); the burned moss/shrub forest had higher species diversity than the mature moss/shrub forest ($\underline{P} = 0.013$); species diversity did not differ between the burn grids ($\underline{P} = 0.674$); and species diversity did not differ between mature grids ($\underline{P} = 0.145$).

Sex, Age, and Reproduction

With 3 exceptions, male:female sex ratios for all species combined did not differ from 1:1; male-biased ratios were obtained for the burned lichen woodland in 1993, the mature moss/shrub forest in 1993, and the burned moss/shrub forest in 1994 (Table 6). Nearly twice as many male red-backed voles as females were captured on the mature moss/shrub forest grid in 1993, but the sex ratio did not differ from 1:1 in 1994 (Table 7). Yellow-cheeked vole sex ratios did not differ from 1:1 for either of the moss/shrub forest grids during the study except on the burned moss/shrub forest in 1994, when no females were captured (Table 8).

Using pooled data from all years, no association was found between the 4 vegetation types and the numbers of immature and adult small mammals captured on them ($X^2 = 0.61$, d.f. = 3, $\underline{P} = 0.894$). Additionally, no difference in the age structures between the burned grids, the mature grids, the lichen woodland grids, or the moss/shrub forest grids were detected in the pooled data for these comparisons (X^2; $\underline{P} > 0.45$). However, in 1993, age structure varied between the burned grids ($X^2 = 7.31$, d.f. = 1, $\underline{P} = 0.007$); fewer immature and more adult small mammals

Table 5. Small mammal species diversity (H'), distribution evenness (J'), and richness for four 100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992–1994.

Vegetation Type	Diversity[1] (H')	Evenness[1] (J')	Richness[2]	n
1992				
Burned lichen woodland	0.45	0.75	4	16
Mature lichen woodland	0	0	1	3
1993				
Burned lichen woodland	0.53	0.88	4	19
Mature lichen woodland	0.30	0.62	3	9
Burned moss/shrub forest	0.52	0.66	6	122
Mature moss/shrub forest	0.43	0.61	5	84
1994				
Burned lichen woodland	0	0	1	6
Mature lichen woodland	0	0	0	0
Burned moss/shrub forest	0.58	0.83	5	29
Mature moss/shrub forest	0.25	0.53	3	17
Overall				
Burned lichen woodland	0.56	0.72	6	41
Mature lichen woodland	0.25	0.52	3	12
Burned moss/shrub forest	0.53	0.69	6	151
Mature moss/shrub forest	0.42	0.60	5	101

[1]Species diversity and distribution evenness measures are determined from the Shannon-Weaver Index (Zar 1974).

[2]Species richness is the number of species detected on each grid from the total captures (n) for that grid.

Table 6. Sex and age ratios for small mammals trapped on four 100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992-1994.

Vegetation Type	Male:Female	*P*[1]	(*n*)	Immature:AF[2]	(*n*)
1992					
Burned lichen woodland	0.8:1	0.402	(16)	6:1	(14)
Mature lichen woodland	2:1	0.500	(3)	2:1	(3)
1993					
Burned lichen woodland	2.2:1	0.084	(19)	1:1	(10)
Mature lichen woodland	1.3:1	0.500	(9)	5:1	(6)
Burned moss/shrub forest	0.8:1	0.010	(119)	2.9:1	(97)
Mature moss/shrub forest	1.7:1	0.136	(81)	3.1:1	(61)
1994					
Burned lichen woodland	0.7:1	0.500	(6)	5:1	(6)
Mature lichen woodland	0:0		(0)	0:0	(0)
Burned moss/shrub forest	4.8:1	0.291	(29)	4.3:1	(16)
Mature moss/shrub forest	1.6:1	0.001	(17)	2:1	(9)

[1]Departure from a 1:1 male:female ratio was determined from a binomial probability distribution (*P*).

[2]Age ratios are expressed as the number of immatures (both males and females) per adult female (AF); the immature age category includes juvenile and subadult animals identified from weight and molt characteristics.

Table 7. Sex and age ratios for red-backed voles (*Clethrionomys rutilus*) captured on four 100 x 100 m grids in burned moss/shrub forest (BMSF) and mature moss/shrub forest (MMSF), Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1993 and 1994.

Vegetation Type	Male:Female	P[1]	(n)	Immature:AF[2]	(n)
1993					
BMSF	0.8:1	0.256	(58)	5.5:1	(52)
MMSF	1.9:1	0.018	(52)	6.8:1	(47)
1994					
BMSF	3:1	0.073	(12)	2:1	(9)
MMSF	1.4:1	0.387	(12)	3:1	(8)

[1]Binomial probability values (P) reflect departure from a 1:1 ratio.

[2]Age ratios are expressed as the number of immatures (both males and females) per adult female (AF); the immature age category includes juvenile and subadult animals identified from weight and molt characteristics.

Table 8. Sex and age ratios for yellow-cheeked voles (*Microtus xanthognathus*) captured on 4-100 x 100 m grids in burned moss/shrub forest (BMSF) and mature moss/shrub forest (MMSF), Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1993 and 1994.

Vegetation Type	Male:Female	P[1]	(n)	Immature:AF[2]	(n)
1993					
BMSF	1.5:1	0.377	(10)	6.8:1	(31)
MMSF	0.9:1	0.371	(37)	2:1	(6)
1994					
BMSF	7:0	0.008	(7)	7:0	(7)
MMSF	0:0	--	(0)	0:0	(0)

[1]Binomial probability values (P) reflect departure from a 1:1 ratio.

[2]Age ratios are expressed as the number of immatures (both males and females) per adult female (AF); the immature age category includes juvenile and subadult animals identified from weight and molt characteristics.

than expected were captured in the burned lichen woodland based on comparison of the expected value with 90% Bonferroni confidence intervals constructed around the observed value (Byers and Steinhorst 1984).

The immature:adult female ratio was most variable on the burned lichen woodland grid, ranging from 6:1 in 1992 during the first year of the study to 1:1 in 1993 when peak population estimates were obtained (Table 6). Both mature grids had the highest number of immatures per adult female in 1993, while the burned moss/shrub forest grid had the highest number of immatures per adult female in 1994 when population estimates were lowest. The number of red-backed vole immatures per adult female declined on both moss/shrub forest grids from 1993 to 1994 (Table 7). Yellow-cheeked vole immatures were relatively numerous on the burned moss/shrub forest grid in both 1993 and 1994, but no adult females were captured there in 1994 (Table 8).

Placental scars and embryos were detected only in red-backed voles and masked shrews during the surveys. Of the females with placental scars or embryos examined during the 3-year study, red-backed voles had a mean of 8.8 placental scars/embryos per female ($\underline{n}$ = 12) and masked shrews had a mean of 6.0 placental scars/embryos per female ($\underline{n}$ = 2). The mean number of placental scars/embryos per red-backed vole female differed between 1993 and 1994 (F = 6.36, $\underline{P}$ = 0.0357). A mean of 8.0 placental scars/embryos per female with placental scars or embryos was obtained for red-backed voles ($\underline{n}$ = 6) in 1993 (when population estimates were high), while a mean of 11.5 placental scars/embryos per red-backed vole female ($\underline{n}$ = 4) was obtained in 1994 (when population estimates were low). All females with placental scars/embryos were captured on the moss/shrub forest grids, except for 2 red-backed voles from the burned lichen woodland grid.

Only 7 animals, all red-backed voles, were lactating at the time of capture. Five lactating red-backed voles were captured on the burned moss/shrub forest site and 2 were captured on the mature moss/shrub forest site. Four of the lactating red-backed voles had perforate vulvae and embryos or recent placental scars. No placental scars or embryos were detected with the unaided eye on lactating animals with imperforate vulvae ($\underline{n}$ = 3).

Capture Rates and Trap Success

Capture rates on the 4 grids ranged from 0 to 13.6 animals per 100 trapnights, with the lowest capture rate coming from the mature lichen woodland and the highest from the burned moss/shrub forest (Table 9). Capture rates declined on all 4 grids from 1993 to 1994, and this decline was most pronounced on the moss/shrub forest grids (Table 9). Snap traps accounted for 59% of the total small mammal captures, but none of the shrews or lemmings were captured in these traps (Table 10). The capture rate for pitfall traps was 0.050 captures per trapnight while that for snap traps was 0.028 captures per trapnight.

There was a relationship between trap type and the age of the small mammal captured in it (X^2 = 19.93, d.f. = 1, $\underline{P}$ = 0.000). Fewer adult animals were captured than expected in snap traps and more adult animals than expected were captured in pitfall traps during the study (Bonferroni confidence intervals, α = 0.05), despite snap traps accounting for 43 of the 49 adult red-backed vole captures during the study and 18 of the 24 adult yellow-cheeked vole captures. Shrews were captured only in pitfall traps, and 60 of the shrews captured ($\underline{n}$ = 68) were identified as adults. Fewer immature animals were captured in pitfall traps; only 27% of

Table 9. Small mammal capture rates (CR) per 100 trapnights for four 100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, August 1992-1994.

Vegetation Type	1992		1993		1994	
	CR[1]	n	CR	n	CR	n
Burned lichen woodland	1.8	16	2.1	19	0.7	6
Mature lichen woodland	0.3	3	1.0	9	0	0
Burned moss/shrub forest			13.6	122	3.2	29
Mature moss/shrub forest			9.3	84	1.9	17

[1]Capture rates were calculated from 3-day trapping periods (900 trapnights per grid).

Table 10. Number of individuals by species captured by trap type on 4-100 x 100 m grids in different black spruce vegetation types in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Alaska, August 1992-1994.

Species	Snap trap	Pitfall trap
Yellow-cheeked vole	54	21
Red-backed vole	124	36
Masked shrew	3	50
Pygmy shrew	0	4
Dusky shrew	0	8
Unidentified shrew	0	1
Northern bog lemming	0	3
Brown lemming	0	1
Total captures	181	124

the immature red-backed voles (n = 111) and 25% of the immature yellow-cheeked voles (n = 24) were captured in pitfall traps. Eight immature shrews were captured, all in pitfall traps.

DISCUSSION

Microtine Populations in Burned Moss/Shrub Forest

Of the 4 black spruce vegetation types sampled, the burned moss/shrub forest was most productive in terms of small mammal abundance and had, along with the burned lichen woodland grid, the highest small mammal species diversity. Small mammal biomass was greatest in the burned moss/shrub forest, primarily due to the abundance of the larger yellow-cheeked voles on the grid. Several factors may have contributed to the abundance and diversity of small mammals on this habitat type: relatively warm, well-drained soils; a moderately thick organic layer; high shrub cover; abundant berry-producing shrubs; and availability of grasses and forbs suitable for winter and summer foods.

Yellow-cheeked voles.--Although red-backed voles were most numerous on the burned moss/shrub forest grid, yellow-cheeked voles accounted for 56-57% of the small mammal biomass, and more yellow-cheeked voles were captured from this area than from the other areas studied. Yellow-cheeked vole populations are associated with good burrowing conditions (West 1979, Wolff and Lidicker 1980), varied microtopography relief (Douglass 1977), and recently burned sites (West 1979). The soil temperature, soil moisture content, and microtopography on the burned moss/shrub forest grid are apparently well suited to yellow-cheeked voles and probably result from the 1978 fire. Removal of overstory vegetation and insulating mosses by wildfire changes the surface albedo of burned areas, which often results in warmer soil temperatures (Viereck and Schandelmeier 1980). These warmer soil temperatures facilitate deeper seasonal thaw levels and soils become drier in some cases (Swanson 1996). This process of soil warming probably occurred on the burned moss/shrub forest grid, since permafrost was not encountered within 1.5 m of the mineral soil. In contrast, permafrost was encountered on the unburned moss/shrub forest grid at 55 cm. Additionally, soils on the burned moss/shrub forest grid did not show evidence of reduction (indicating wet soils) until 30 cm depth in one soil core and 60 cm in the other, but soils on the mature moss/shrub forest were saturated with water below 12 cm.

The warmer and drier soils present on the burned moss/shrub forest grid (and on burned sites in general) may serve as optimal substrate for runway and colony construction and hence support a relatively high population of burrowing small mammals (when sufficient food is available). Rhodes and Richmond (1985) found that burrowing medium was of considerable importance to pine voles (*Microtus pinetorum*), and they preferentially chose loam/peat moss burrowing substrate where tunnel integrity, reduced resistance to burrowing, and soil moisture factors were optimum. The high percentage of moss cover and moderately deep organic layer on this grid would provide similar burrowing and digging properties. Small mammal density has also been correlated to organic mat depth in Ontario (Morris 1979) and in the upper Kobuk River valley (Swanson 1996).

Plant composition is probably an important factor in establishing and maintaining yellow-cheeked voles on the burned moss/shrub forest. West (1979) found a correlation between plant taxa prominent in early successional post-fire stages and the presence of *Microtus* species. In response to high nutrient availability, plant productivity on recently burned black spruce sites is high, particularly for common post-fire plant species such as fireweed (*Epilobium* spp.), bluejoint (*Calamogrostis canadensis*), and horsetail (*Equisetum* spp.) (Viereck and Schandelmeier 1980, Viereck 1983). These post-fire plant species are primary food sources for yellow-cheeked voles and are critical for colonization of recent burns by this species. Summer foods for yellow-cheeked voles consist of horsetail, graminoids, dicots (forbs), and berries (West 1979, Wolff and Lidicker 1980), which were common on the burned moss/shrub forest grid. More graminoids and forbs were found on the burned shrub/moss forest than on the other vegetation types studied (Appendix I), enabling it to support a high yellow-cheeked vole population.

Yellow-cheeked voles also require a supply of fireweed and horsetail rhizomes for winter food caches (Wolff and Lidicker 1980). Since horsetail, bluejoint and fireweed spread into post-fire areas primarily via rhizomes growing in mineral soil (Viereck and Schandelmeier 1980), burn sites should support a plentiful supply of rhizomes for winter food caches (unless fire intensity is high and rhizomes are destroyed). Fireweed and horsetail were relatively abundant in the burned moss/shrub forest grid (Appendix I), and Swanson (1996) found horsetail to be a common and relatively abundant forb on most burns <50 years old (except on dry sites) in the Kobuk Preserve Unit. Burn sites retain a well-developed herbaceous layer until the canopy closes late in the tall shrub sapling stage (sometime within 50 years post-fire; Foote 1983); since trees in the burned moss/shrub forest site (16 years post-fire) were still seedling/small shrub height and the canopy was not closed, the herbaceous layer was still well-developed during the study.

Red-backed voles.--Because red-backed voles are habitat generalists and are found uniformly distributed in many different forest types (West 1979, Krebs and Wingate 1985), their abundance in the burned moss/shrub forest is likely related to food availability. Red-backed voles rely heavily on berries for food during all seasons of the year and also consume fungi, moss (during early summer before berry ripening), arthropods, lichens (spring) and some dicot leaves (West 1979, Bangs 1984). Berry-producing shrubs [blueberry (*Vaccinium uliginosum*), lowbush cranberry (*V. vitis-idaea*), and crowberry (*Empetrum nigrum*)] were more abundant on the burned moss/shrub forest site than on the other areas studied; the high red-backed vole numbers on this grid were likely correlated to its high berry production. Mushrooms, which are particularly important during years of poor fruit production (West 1978), were found throughout the grid area, and many bore signs of rodent consumption.

The diet of red-backed voles differs significantly from that of *Microtus* species (West 1978), potentially allowing coexistence of high populations of both red-backed and yellow-cheeked voles on the burned moss/shrub forest site. Stomach contents for yellow-cheeked voles examined during the study consisted of green vegetation (supporting the importance of graminoids and forbs in their diet) while stomachs of red-backed voles in the same area were consistently full of blueberries. No evidence of interspecific conflict was observed and both species were caught in the same traps set along prominent small mammal runways.

Microtine Populations in Mature Moss/Shrub Forest

Small mammal abundance and biomass on the mature moss/shrub forest site was lower than on the burned moss/shrub forest site but much higher than on the lichen woodland grids.

Yellow-cheeked voles.--Although yellow-cheeked voles are generally associated with burn sites (West 1978, Wolff and Lidicker 1980, Johnson and Paragi 1992), they are also consistently found along waterways and lakes in taiga areas where flood and ice disturbance maintains a dense growth of graminoids and light-seeded, quickly developing plants (West 1978). These small areas of consistent habitat may be easily overpopulated, causing immature animals to disperse in search of other suitable disturbed sites. West (1979) speculated that a few *Microtus* might be sustained where toppled trees allowed light to reach the forest floor and enhance herbaceous growth. The northeast corner of the mature moss/shrub forest grid, where canopy cover was <10% (in contrast to 25-50% closure elsewhere on the grid) and *Carex* was abundant, may have served as a small pocket of suitable yellow-cheeked vole habitat; all yellow-cheeked voles captured on the grid were from this corner. Burrowing conditions were good in the 18-21 cm organic layer, but soils were frozen and wet below this layer. Graminoid and forb abundances may have been insufficient to sustain a larger yellow-cheeked vole population. No yellow-cheeked voles were captured on this grid in 1994 when small mammal populations dropped throughout the study area. It is unclear whether small mammal trapping in 1993 eliminated this population of yellow-cheeked voles or some other factor affected their overwinter survival and/or summer reproductive efforts in 1994.

Red-backed voles.--Three times as many red-backed voles as yellow-cheeked voles were taken from this grid, and red-backed voles comprised 59% and 96% of the biomass in 1993 and 1994 respectively. The greater proportion and biomass of red-backed voles is probably more a function of the habitat being unsuitable for yellow-cheeked voles (as previously discussed) rather than being highly preferred by red-backed voles. The actual number of red-backed voles taken from the mature moss/shrub forest grid and the burned moss/shrub forest grid were nearly the same, but yellow-cheeked vole numbers were much lower on the mature moss/shrub forest (Table 2).

West (1979) found red-backed voles uniformly distributed in all successional stages but felt that mature forest stands harbor the source populations for recolonization of disturbed areas. Berry-producing shrubs were abundant and apparently able to support a sizable population of red-backed voles; forbs and graminoids were also available but not in abundance. Mosses, which may be an important food source for red-backed voles in early summer after previous year berries have been consumed and before current-year berries are available (West 1979), were also abundant on the mature moss/shrub forest grid. Moss was also important in forming the deep organic layer which red-backed voles used extensively for burrowing; moss hummocks in the southwest corner of the grid were riddled with vole burrows and trails.

Microtine Populations in Burned Lichen Woodland

The impacts of fire on small mammal populations, particularly the long-term effects, are hard to predict. In the short term, fire behavior, intensity, and size determines the habitat conditions within a burn, the proximity of plant and animal source populations, and the recolonization rates of small mammals into burn areas. The 1991 fire that burned through the lichen woodland area left burned lichen ground cover and bare mineral soil over much of the area, but unburned sphagnum moss hummocks and willow swales were interspersed throughout the burn. Riparian habitat was also largely intact within 3-4 m of streams. Riparian areas and unburned swales within 600 m of the grid were heavily populated with voles and shrews in 1993 during the first year of the study (Swanson 1993). These unburned habitat patches probably served initially as refugia for voles and shrews displaced by the fire and later as a recruitment source for the burned area as vegetation and habitat conditions improved.

Small mammal diversity on the burned lichen woodland grid was relatively high but probably reflects transient animals either passing through or conducting temporary foraging trips into the burn. Overcrowding in the relatively small unburned habitat patches also may have forced less social species such as the northern bog lemming and brown lemming out into the burn area, resulting in higher diversity indices in this probable lower quality habitat.

Yellow-cheeked voles.--All yellow-cheeked voles captured on the burned lichen woodland grid came from a colony established in the southeast corner. It is unclear whether the colony existed prior to the 1991 fire, but the tremendous increase in excavations in and around the colony between the first and second year of the study indicates an expanding colony. The colony was situated on an unburned sphagnum moss area so digging conditions at the colony site were good and downed trees and sphagnum moss hummocks provided sufficient escape cover. Forb and graminoid availability was low during the first year of the study but increased slightly during the second and third years. Rhizomes growing in mineral soil often survive fire and were probably available for vole consumption.

Diet and burrowing conditions may enable yellow-cheeked voles to establish residency in burned areas prior to red-backed voles. Rhizomes for winter food sources and early successional forbs and grasses for summer foraging are often available well before berry production would enable red-backed voles to overwinter on a recent burn (see discussion on red-backed voles and overwintering below). Food sharing and communal nesting by yellow-cheeked voles in winter may also speed residency establishment on burns. Food caches established during the summer provide 90% of winter foods, which means less time and energy spent in foraging activity (Wolff and Lidicker 1981). Communal nesting would also decrease the amount of energy expended per individual to maintain body temperatures.

Red-backed voles have also been known to aggregate in thicker moss layers during midwinter in areas where overwintering habitat is limited (West 1977). However, food sources would soon be depleted in the local area of the aggregation (since red-backed voles do not establish food caches), thereby necessitating increased foraging time and energy expenditure. Thus, while the communal nesting system used by yellow-cheeked voles may increase their survival potential and ability to establish themselves in a recent burn, the aggregation system employed by red-backed voles in marginal habitat appears to have only a short-term benefit and does not necessarily increase long-term fitness and survival. A communal nesting and food sharing system may have enabled yellow-cheeked voles to persist on the burned lichen woodland grid in 1994 when other small mammal species on the grid either died off or dispersed from the site.

Red-backed voles.--Few red-backed voles were captured on the burned lichen woodland grid during the first 2 years post-fire and none were captured during the third year when population numbers dropped on all 4 grids. West (1982) found that until 6 years post-fire, only immigrant pregnant female and transient red-backed voles used a burn in interior Alaska. Whether the 3 adult females captured on this grid were immigrants is unknown, but all exhibited some sign of pregnancy--2 had embryos and the third had large mammaries, possibly indicating pregnancy though no embryos or placental scars were visible. Seven immatures (2 females and 5 males) and 2 sexually mature adult males were also captured and were likely transients or dispersers from nearby communities. Immature animals are often forced to disperse into less desirable habitat by territorial adult animals in densely populated optimal habitat, so the relatively high number of immatures may indicate marginal habitat conditions on the burned lichen woodland grid. Depending on site food and cover conditions, red-backed voles can recolonize burns relatively fast, since source populations exist in nearly all habitats (West 1982).

Food and escape cover seem to be the primary factors limiting recolonization of burns by red-backed voles. Red-backed voles using a burn in interior Alaska abandoned it each year in midwinter until sufficient food resources (berries and lichens) developed to allow overwintering (West 1982). On the burned lichen woodland grid, blueberry bushes growing on sphagnum moss hummocks survived the fire and were the primary berry-producers on the site; lowbush cranberry was also present in small quantities. Percent cover for these 2 berry shrubs was 5-25% on the grid, but berry production was probably insufficient to support an overwintering population of red-backed voles.

Herbaceous escape cover is necessary to protect voles from predation while foraging (Birney et al. 1976). Minimal escape cover on the burned lichen woodland habitat may result in high predation pressure on voles and slow recolonization. Red-backed vole activity would tend to center around unburned sphagnum moss hummocks where berries were available as well as some cover. Predators such as weasels and raptors in the area would quickly key in to these activity centers and capture voles on the hummocks or in transit between them.

Microtine Populations in Mature Lichen Woodland

The mature lichen woodland grid had the lowest abundance of small mammals and the lowest species diversity of all 4 black spruce types examined. Only 3 species were taken from this grid, and with the exception of 1 dusky shrew and 1 masked shrew, all animals captured were red-backed voles. No animals were captured on the grid during the low small mammal population year in 1994.

Yellow-cheeked voles.—Lack of escape cover, food, and good digging conditions on the mature lichen woodland grid apparently precluded habitation by yellow-cheeked voles. Yellow-cheeked voles have been positively correlated with areas of greater micro-relief where herbaceous escape cover was abundant (Douglass 1977); herbaceous escape cover was particularly important in forests with moss- or lichen-dominated understory (such as that on the mature lichen woodland site). Very little vertical herbaceous escape cover was available on this grid. Food sources associated with yellow-cheeked voles on the other grids in the study (*Equisetum* spp., *Epilobium* spp., and graminoids) were also absent or present only in small quantities (Appendix I). Fireweed seldom persists into the mature black spruce stage (Foote 1976, Swanson 1996) and *Equisetum* cover is generally low on mature black spruce forest on permafrost (Swanson 1996). *Carex* spp. can be relatively abundant in mature black spruce forest on permafrost (Swanson 1996) but it was sparse on this site.

The organic layer on this grid was the thinnest of the 4 grids studied, and moss only accounted for 1-5% of the ground cover. Thus, burrowing conditions for yellow-cheeked voles on this grid were marginal at best.

Red-backed voles.--Although blueberry and lowbush cranberry production on the mature lichen woodland could probably support a small population of red-backed voles, lack of burrows, trail systems, and animals indicate little use of the area. Lack of escape cover, either in the herbaceous or moss/organic layers, may inhibit voles from using the area, though red-backed voles are probably better able to use trees for escape cover than yellow-cheeked voles. The fact that no red-backed voles were taken during the low population year indicates that the habitat is marginal even for these habitat generalists, since animals in low density, marginal habitats would tend to disappear first during times of hardship. Swanson (1996) also found microtine sign to be rare in lichen-dominated habitats.

Shrew Populations

Masked shrews were the most abundant shrew captured during the study, as it was in studies in Manitoba (Wrigley et al. 1979) and interior Alaska (Johnson et al. 1995). The masked shrew comprised 70.1% of the shrews captured in Manitoba and often rivaled microtine species for the most abundant species captured (Wrigley et al. 1979). Masked shrews are generalists, utilizing a wide variety of habitats and feeding on a broad array of invertebrates (Jones and Birney 1988). In addition, masked shrews have relatively high reproductive rates for shrews, producing 2-5 litters per year, with 4-10 young per litter (Hazard 1982, Jones and Birney 1988). These factors enable masked shrews to exploit all habitat types available in an area and probably explain why the species was found in all 4 black spruce vegetation types sampled in this study.

Information on the life histories and ecological roles of the pygmy and dusky shrews is scarce. Pygmy shrews were captured only on the moss/shrub forest grids, which may indicate habitat selectivity. The low reproductive rate for pygmy shrews (1 litter per year of 3-8 young) may explain the low number (8) of pygmy shrews encountered during the study (Hazard 1982, Jones and Birney 1988). The dusky shrew was the rarest shrew captured during the study. One dusky shrew was captured on each of the 4 grid sites, suggesting that they are habitat generalists. Reproductive rates for the dusky shrew are not known but are assumed to be low, and Wrigley et al. (1979) found that dusky shrews were not common anywhere in Manitoba.

In addition to low reproductive rates, Wrigley et al. (1979) attributed the rareness of the pygmy and dusky shrews to the abundance and great ecological amplitude of the masked shrew. Hazard (1982) felt that there probably is some unknown habitat component that the pygmy shrew exploits relatively efficiently which enables it to coexist with more abundant shrew species (such as the masked shrew). Resource partitioning between shrew species has been observed in shrew communities in Siberia (Churchfield and Shelftel 1994) and New Brunswick (Whitaker and French 1984) and may facilitate coexistence between pygmy and masked shrews in Alaska.

Shrews are found in a wide variety of habitats, but areas with high relative humidity and in close proximity to water sources are associated with higher shrew abundances (Getz 1961, Long 1972, Jones and Birney 1988). The moss/shrub forest grids produced by far the highest abundance of shrews, and the dense moss cover and depth of the organic layer in these habitat types probably provide optimal humidity conditions for shrew habitation. Furthermore, standing water was available at the southeastern end of the mature moss/shrub forest grid. Open water was present approximately 300 m from the burned moss/shrub forest grid, probably too far away to be used by shrews in the immediate grid vicinity.

Shrew species diversity and abundance in Manitoba was a function of both moisture levels in the microhabitat and the abundance of invertebrates and plant foods (Wrigley et al. 1979). Shrews feed on a broad array of invertebrates, both adult and larval forms (Jones and Birney 1988, Whitaker and French 1984). Adult and larval stages of beetles (Order Coleoptera), flies (Order Diptera), moths and butterflies (Order Lepidoptera), and spiders (Order Araneida) were the primary components of shrew diets in New Brunswick (Whitaker and French 1984). Beetle and fly larvae are typically found on or in the ground, in rotting vegetation, and under stones and bark (Borror and White 1970); many larval forms of these two insect orders are aquatic, which may explain shrew affinity for open water. In addition to insects, shrews also may eat meat, if available. Shrews are capable of killing other small mammals [particularly juveniles and nestlings (Timm 1975)], but are more likely to eat carrion (Hazard 1982). Carrion availability for potential shrew consumption would be relatively high in areas with dense vole populations, such as those on the moss/shrub forest grids. Shrews use rodent runways and burrows as feeding routes (Vaughan 1986); areas with high vole populations and extensive runway systems (as on the moss/shrub forest grids) presumably would provide optimal foraging conditions for shrews.

Arthropod densities on the 4 study grids were not examined, but the abundance of downed wood and litter on the burned moss/shrub forest grid probably harbored an abundant supply of insects and larvae for shrew consumption. The decaying moss at the bottom of the thick moss layer on the mature moss/shrub forest grid also probably hosts numerous adult and larval arthropods.

Shrew densities were very low on the burned lichen woodland grid, even though more arthropods are found on recent burns than on unburned control sites (Viereck and Dyrness 1979). Martell (1984) also found abundant arthropods but few shrews in a lightly burned area with some trees and scorched moss in Ontario. Getz (1961) and Buckner (1964) found that food abundance and shrew density did not appear to be directly correlated and that various shrew species could be abundant, scarce, or absent irrespective of prey (insect) densities. The low shrew density on the burned lichen woodland grid could be attributed to the presence of a low humidity microclimate, as found by Fox (1983) when studying shrew populations on poorly vegetated, early-successional habitats. The burned lichen woodland grid had isolated unburned sphagnum moss hummocks throughout, but traversing the low-cover, low-humidity burned soils between these potentially acceptable but small habitat patches may have deterred shrews from using the area.

Low shrew abundance in the mature lichen woodland habitat was probably due to several factors: 1) the open lichen understory provided little cover for foraging shrews or for escape cover; 2) the relatively thin organic layer was marginal for shrew burrowing; 3) arthropod density may have been low due to the lack of rotting vegetation or downed wood; and 4) because microtine populations were very low or nonexistent in this habitat type, shrews would not have access to microtine carrion or a microtine tunnel/trail system for travel and foraging activities.

Small Mammal Population Fluctuations

The short duration of this study precludes discussion of multi-year cycling; however, a marked population decline was observed and merits some discussion. According to local trappers, spring small mammal sign was abundant in the Kobuk River area in 1993 (which corresponds to the high fall population detected in this study in 1993), but little sign was observed in spring 1994 when small mammal populations on the grids were also low (G. Bamford and D. Schmitz, trappers, pers. commun.). In addition to the obvious drop in small mammal abundance from 1993 to 1994, changes in litter size and immature:adult ratios occurred. Red-backed vole litter size (based on placental scars) increased in 1994 when populations were low; mean placental scars increased from 8.0 in 1993 to 11.5 in 1994. Low litter size has also been found in high density shrew populations (Buckner 1966). In spite of this apparent increased reproduction, the immature:adult female ratios for red-backed voles on the moss/shrub forest grids declined, indicating poor juvenile survival. Immature:adult female ratios for yellow-cheeked voles also declined on the moss/shrub forest grids. On the burned moss/shrub forest grid a high number of immature yellow-cheeked voles (relative to adult females) were taken in 1993, but in 1994 only 7 immatures were captured and no adult females were taken; this suggests transient animals dispersing in from adjacent areas rather than being produced on the grid site.

The high litter size obtained in this study may be indicative of a population compensating for high mortality by maximizing natality rates, as was found for red-backed voles in Northwest Territories (Martell and Fuller 1979); the reduction in immatures further suggests a high mortality rate. The cause of this high mortality is unknown, but it affected all small mammal species in all habitats sampled in this study. The mortality factor affected a large region as small mammal population declines were also documented on the Kanuti National Wildlife Refuge south of the study area (A. Zirkle, U.S. Fish and Wildl. Serv., pers. commun.) and the Nowitna National Wildlife Refuge to the southwest (W. Johnson, U.S. Fish and Wildl. Serv., pers. commun.).

Species diversity indices on all grids except the burned moss/shrub forest grid were lower in 1994 than in the other years of the study and suggest low small mammal population levels. During a large scale decline in small mammal populations, chances of capturing low density species (such as pygmy and dusky shrews or northern bog and brown lemmings) or those in marginal habitats (i.e., the yellow-cheeked voles in the mature moss/shrub woodland) are much lower, thus producing lower diversity indices. The absence of large yellow-cheeked voles in 1994 also indicates a low population density. Douglass (1977) reported that yellow-cheeked voles >90 gm were captured only during high population densities in Northwest Territories. During 1993, when population estimates were high, 2 yellow-cheeked voles weighing 120 gm and 124 gm were captured on the burned moss/shrub forest grid; only 2 adult voles were captured during 1994 and neither weighed more than 50 gm.

Trap success for 1994 may have been influenced by inclement weather during the trapping period. Weather conditions during the trapping period in 1994 included record rainfall, extreme flooding along the Kobuk River, and temperatures below freezing during the day. The numbers of snapped traps and flooded cones on the lichen woodland grids were 15 times higher in 1994 than in 1993, but incidental trap closure on the moss/shrub forest grids was comparable between the 2 years. The low capture rates obtained in 1994 on the lichen woodland grids may partially be explained by sprung traps or flooded cones, but trap closure would not explain the lowered capture rates on the moss/shrub forest grids.

Some residual effect of removal trapping the same grids in consecutive years may have influenced abundance estimates, but given the short life cycle of small mammal species and the small size of the grids relative to available habitat, it is unlikely that a significant impact was made.

Predator/Prey Implications

Optimal feeding habitat for predators that depend on small mammals for food should have high small mammal density, sufficient vegetative escape cover for predators and prey, and coarse woody debris to allow winter subnivean access to small mammal populations (Sherburne and Bissonette 1994). Avian predators may additionally require perching sites and minimal overstory (shrub) cover for ease of small mammal detection and capture. Korpimaki and Norrdahl (1991) found that high microtine density areas experience rapid immigration of kestrels and short-eared owls, usually nomadic adults. Identification of high density vole areas by diurnal raptors may result from their ability to detect ultraviolet light, which is reflected from vole urine and feces used to mark above-ground runways; kestrels searching from the air can easily locate high density vole areas, particularly in the spring when vegetation is not fully leafed out (Viitala et al. 1995). The ability to detect and evaluate vole abundance through feces and urine concentrations would enable raptors to efficiently locate feeding areas and exploit high density vole areas such as the burned moss/shrub forest in this study.

The burned moss/shrub forest habitat had the highest small mammal density and biomass and should be able to support a relatively high predator population. The presence of standing and downed dead trees from the burn provided optimal perching sites for raptors as well as subnivean access for weasels and marten. Perching kestrels were observed on the grid during the study. The incomplete canopy closure on the burned moss/shrub forest grid area would facilitate detection of vole runways from the air as previously discussed. The burned moss/shrub forest grid was also the only grid where marten scat was found.

Small mammal (prey) density was also high on the mature moss/shrub forest, making it a desirable feeding habitat for predators. Mammalian predators may be better able to utilize this habitat because tree cover (25-50% closure) may inhibit mobility and visibility for avian predators. The multi-strata black spruce trees on the grid plus the coarse woody debris generally accumulated in older forests should provide effective winter foraging access for marten and weasels (Sherburne and Bissonette 1994).

According to a local trapper, marten sign in the vicinity of the lichen woodland grids has never been abundant and most marten using the area appear to be transient rather than resident animals (G. Bamford, trapper, pers. commun.). Small mammal density is probably the limiting factor for marten and weasel abundance in this area. As the burned lichen woodland vegetation recovers, food and cover conditions for small mammals may improve, supporting higher small mammal populations and, hence, more marten and weasels.

Predictably, the general small mammal population decline in 1994 was accompanied by decreased marten numbers. Marten sign in the Kobuk Preserve Unit and trapper success in obtaining marten along the south side of the Brooks Range in general was very low during the 1994-95 trapping season and coincided with the small mammal decline observed during 1994 fieldwork (G. Bamford and D. Schmitz, trappers, pers. commun.). In addition to changes in marten productivity and survival caused by small mammal scarcity, vole population crashes can also cause wide emigrations of predators from their normal ranges (Viitala et al. 1995). Local trappers have mentioned "marten waves" moving through their trapping areas in other years, and this movement of marten through new territory may have been in response to low small mammal abundance in their normal ranges.

To better understand the actual predator/prey relationships in the post-fire black spruce seral stands in the Kobuk Preserve Unit, predator density information would have to be collected concurrently with small mammal population data for the habitat types examined in the study.

SUMMARY

1) Seven small mammal species were identified during the study: yellow-cheeked vole, red-backed vole, masked shrew, pygmy shrew, dusky shrew, northern bog lemming, and brown lemming. Red-backed voles were most abundant, followed by yellow-cheeked voles and masked shrews, respectively.

2) Snap traps accounted for 59% of the total captures; however, shrews and lemmings were captured only in pitfall traps.

3) Burned vegetation grids had higher species diversity than their corresponding mature vegetation grids.

4) Small mammal abundance was highest on the burned moss/shrub forest and lowest on the mature lichen woodland. Small mammal abundance was higher on the moss/shrub forest grids than on the lichen woodland grids.

5) Small mammal populations declined significantly from 1993 to 1994 on all 4 grid habitats. Low small mammal abundance was noted on other small mammal study sites in interior Alaska in 1994.

6) Placental scars and embryos were detected only in red-backed voles and masked shrews. When populations were high in 1993, the mean red-backed vole litter size was 8.0, but when populations were low in 1994, mean litter size was 11.5. Increased natality is often a response to high mortality (when food is not the limiting factor).

7) Small mammal abundance on post-fire seral stages is likely related to food availability, organic mat depth (burrowing/digging substrate), and presence of escape cover.

8) Yellow-cheeked voles probably are found in disturbed areas such as burns because of better soil conditions for colony and runway formation and the presence of forbs and graminoids. Common post-fire plant species such as *Equisetum* spp., *Epilobium* spp., *Carex* spp., and *Calamagrostis canadensis* are primary food sources for these voles. Rhizomes produced by these plants (which often survive fires since they grow in mineral soil) are cached for winter consumption and enable yellow-cheeked voles to establish themselves and overwinter on burned areas prior to other vole species establishing residency.

9) Red-backed voles are found in a wide variety of habitats, but they are probably most abundant in areas with a well-developed organic layer for tunneling, high berry production, and sufficient escape cover.

10) Red-backed voles appear to focus on berries while yellow-cheeked voles concentrate on herbaceous vegetation; this potential division of food resources may allow fairly high populations of both species to coexist if adequate supplies of both berries and herbaceous vegetation are available. This situation was encountered in the burned moss/shrub forest habitat.

11) Yellow-cheeked voles were more numerous than red-backed voles in the recently burned lichen woodland grid because berry production was probably insufficient to support a higher population of red-backed voles. Sparse berries would particularly preclude overwintering of red-backed voles in recent burns.

12) Shrews were most abundant on the moss/shrub forest grids, where the organic layer depth, humidity conditions, arthropod abundance, and vole runway/burrow density (for food routes) may have been optimal conditions for shrew habitation.

13) For predators dependent on small mammal food sources, optimal feeding habitat presumably would have a high density small mammal population, coarse woody debris to allow subnivean access to small mammals in the winter, and presence of perching sites and relatively low overstory cover for avian predators. Based on these assumptions, predators in the burned moss/shrub forest habitat would have greater hunting success than on the other sites studied. Mammalian predators may be better suited than avian predators to hunt on the mature moss/shrub forest because tree and canopy cover may deter avian visibility and maneuverability.

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Appendix I. Habitat components and cover class information for 4-100 x 100 m small mammal trapping grids in the Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 1992-93.

Table IA. Habitat components and cover classes from a 10 x 10 m plot within a small mammal trapping grid in burned lichen woodland vegetation, Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 19 August 1992.

Plant Species	Cover Class[a]
Bare soil, litter, and mulch	I
Lichens	IV
Cladina rangiferina	IV
Cladina stellaris	II
Nephroma arcticum	I
Cladonia deformis	+
Mosses	II
Sphagnum spp.	II
Polytrichum spp.	I
Marchantia polymorpha	+
Forbs	I
Chamaedaphne calyculata	I
Equisetum sylvaticum	I
Epilobium angustifolium	+
Graminoids	I
Carex spp.	I
Shrubs	II
Ledum palustre	II
Vaccinium uliginosum	II
Betula glandulosa	+
Vaccinium vitis-idaea	+
Trees	II
Picea mariana	II

[a]Cover classes are as follows:
+ = <1% cover
I = 1-5% cover
II = 5-25% cover
III = 25-50% cover
IV = 50-75% cover
V = >75% cover

Table IB. Habitat components and cover classes from a 10 x 10 m plot within a small mammal trapping grid established in mature lichen woodland, Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 20 August 1992.

Plant Species	Cover Class[a]
Litter and mulch	II
Lichens	IV
Cladina rangiferina	III
Cladina stellaris	III
Cladina mitis	II
Polytrichum spp.	I
Nephroma arcticum	I
Cetraria cucullata	+
Cetraria islandica	+
Nephroma expallidum	+
Cladonia spp.	+
Mosses	I
Pleurozium schreberi	I
Forbs	I
Equisetum arvense	+
Equisetum sylvaticum	+
Lycopodium complanatum	+
Graminoids	I
Carex spp.	I
Shrubs	II
Vaccinium uliginosum	II
Vaccinium vitis-idaea	I
Ledum palustre	I
Trees	III
Picea mariana	III

[a]Cover classes are as follows:
+ = <1% cover
I = 1-5% cover
II = 5-25% cover
III = 25-50% cover
IV = 50-75% cover
V = >75% cover

Table IC. Habitat components and cover classes from a 10 x 10 m plot within a small mammal trapping grid established in burned moss/shrub forest, Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 22 August 1993.

Plant Species	Cover Class[a]
Litter and mulch	II
Lichens	II
Cladonia spp.	II
Crustose lichens	I
Mosses	IV
Polytrichum spp.	IV
Dicranum spp.	I
Forbs	II
Equisetum sylvaticum	II
Epilobium angustifolium	I
Petasites frigidus	+
Graminoids	II
Carex bigelowii	II
Calamagrostis spp.	+
Shrubs	IV
Vaccinium uliginosum	IV
Ledum palustre	IV
Vaccinium vitis-idaea	II
Betula glandulosa	II
Salix glauca	I
Empetrum nigrum	+
Spiraea beauvardiana	+
Trees	II
Picea mariana	II

[a]Cover classes are as follows:
+ = <1% cover
I = 1-5% cover
II = 5-25% cover
III = 25-50% cover
IV = 50-75% cover
V = >75% cover

Table ID. Habitat components and cover classes from a 10 x 10 m plot within a small mammal trapping grid established in mature moss/shrub forest, Kobuk Preserve Unit, Gates of the Arctic National Park and Preserve, Brooks Range, Alaska, 22 August 1993.

Plant Species	Cover Class[a]
Litter and mulch	I
Lichens	IV
Cladina rangiferina	II
Cladina stellaris	II
Cladina mitis	I
Nephroma arcticum	I
Cetraria cucullata	I
Cladonia spp	I
Peltigera spp.	I
Bryoria spp.	I
Cetraria spp. (dark variety)	+
Crustose lichens	+
Mosses	III
Sphagnum spp.	II
Pleurozium schreberi	II
Polytrichum spp.	I
Hylocomium splendens	I
Dicranum spp.	I
Aulacomnium palustre	+
Forbs	I
Equisetum sylvaticum	I
Graminoids	II
Carex bigelowii	II
Shrubs	III
Vaccinium uliginosum	III
Betula glandulosa	II
Empetrum nigrum	II
Ledum palustre	II
Vaccinium vitis-idaea	II
Trees	II
Picea mariana	II

[a]Cover classes are as follows:
+ = <1% cover
I = 1-5% cover
II = 5-25% cover
III = 25-50% cover
IV = 50-75% cover
V = >75% cover

Appendix II. Recommendations for future inventory and monitoring study on small mammal populations in Gates of the Arctic National Park and Preserve, Brooks Range, Alaska.

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1) Assess small mammal diversity in additional habitat types in the Kobuk Preserve Unit, particularly wetland habitats and other unique plant communities such as the Nutuvukti Fen, the tussock tundra ecotonal area, and the mudboil lichen/shrub community south of Selby Lake. *Sorex minutisimus* a rare shrew, recently discovered in North America, was trapped on the Nowitna National Wildlife Refuge south of the park and preserve and may be found in the Kobuk Preserve Unit. Rare species and their habitats should be documented prior to any transportation corridor construction. Transects of snap and pitfall traps could be established and operated for several days during the fall when populations are highest; some species are not captured in snap traps, so pitfall traps are also necessary to ensure adequate sampling and collection of all species in the targeted habitat type. Representative specimens should be collected, prepared as study skins and skeletons, and housed in the University of Alaska Fairbanks Museum to ensure proper documentation.

2) Begin inventorying small mammal species in other habitat types in the park outside of the Kobuk Preserve Unit. Tundra habitats, wetland areas, and additional boreal forest habitats should be examined to better understand the distribution of small mammal species in the park and preserve. Transects of snap and pitfall traps could be established and operated for several days during the fall when populations are highest; some species are not captured in snap traps, so pitfall traps are also necessary to ensure adequate sampling and collection of all species in the targeted habitat type. Representative specimens should be collected, prepared as study skins and skeletons, and housed in the University of Alaska Fairbanks museum to ensure proper documentation.

3) Design a study to examine small mammal population densities and corresponding winter use of those areas by marten. Small mammal population estimates will require grid trapping techniques and data analysis procedures such as those outlined in this report. Marten use of areas could be assessed through winter track counts or by working with a local trapper and examining the marten harvest in the same area the small mammal work was completed. Harvest data for marten from 1988-1993 indicated declining marten populations in the park and preserve vicinity (Swanson 1994); information on prey abundance (small mammals) is needed to determine if marten declines are related to food scarcity.

4) Continue to pursue joint publication of small mammal data collected in the cooperative study between Gates of the Arctic National Park, Koyukuk/Nowitna National Wildlife Refuge, and Kanuti National Wildlife Refuge.

5) Present information from this study at the Northern Furbearer Conference via poster or paper presentation. An article for *Park Science* is also recommended.

As the nation's principal conservation agency, the Department of Interior carries the responsibility of managing most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving our environment, and providing for outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interest of all citizens. The Department also encourages stewardship of our public lands by promoting responsible citizen participation in their care.

March 1996