

Ecological Distribution of Small Mammals in the De Long Mountains of Northwestern Alaska

RICHARD J. DOUGLASS¹

ABSTRACT. The ecological distribution of small mammals (<200 g) was studied in the foothill tundra of the De Long Mountains in northwestern Alaska. Three species of shrews and five species of microtine rodents were trapped on 15 live-trapping grids during 1978 and 1979. Emphasis was placed on the three most abundant microtine species (*Clethrionomys rutilus*, *Microtus oeconomus* and *M. gregalis*).

During late summer up to six species of small mammals were captured per habitat type which ranged from wet meadow through mesic shrubland to dry ridges. Following snowmelt most habitats contained only a single species and some contained none. Only four habitat types were continuously occupied by small mammals during both summers. Species diversity was variable among habitats.

Most species of small mammals were captured on eight or fewer of the 15 trapping grids. Only *Clethrionomys rutilus* was captured on all grids. The number of habitats occupied by *Clethrionomys rutilus* increased from 4 to 14 as population densities increased. The number of habitats occupied by the other species seemed to be independent of population density.

Average population densities for the microtines were low (< 15·ha⁻¹) and, for each species, varied according to habitat type. Only *Clethrionomys rutilus* populations demonstrated marked intra-annual fluctuations (3·ha⁻¹ to 37·ha⁻¹).

Key words: rodents, habitat, Alaska, populations, *Clethrionomys rutilus*, *Microtus oeconomus*, *Microtus gregalis*

RÉSUMÉ. La distribution écologique de petits mammifères (200 g) fut étudiée dans la toundra des contraforts des montagnes De Long dans le nord-ouest de l'Alaska. Trois espèces de musaraignes et cinq espèces de rongeurs microtinés furent capturés dans des grilles à pièges à récipient en 1978 et 1979. L'étude porta surtout sur les trois espèces prédominantes de microtinés (*Clethrionomys rutilus*, *Microtus oeconomus* et *M. gregalis*).

Vers la fin de l'été, jusqu'à 6 espèces de petits mammifères furent capturés par habitat, ce dernier variant entre des prés fonte des neiges, la plupart des habitats ne contenaient qu'une seule espèce et certaines n'en contenaient aucune. Seulement quatre genres d'habitats étaient continuellement occupés au cours des deux étés. La diversité des espèces variait parmi les habitats.

La plupart des espèces de petits mammifères furent capturés sur 8 ou moins des 15 grilles de prise au piège. Seul le *Clethrionomys rutilus* fut capturé dans toutes les grilles. Le nombre d'habitats occupés par le *Clethrionomys rutilus* augmenta de 4 à 14 à mesure que les densités de population augmentaient. Le nombre d'habitats occupés par les autres espèces semblait être indépendant de la densité de population.

La densité moyenne de population pour les microtinés était peu élevée (15·ha⁻¹) et variait pour chaque espèce selon le genre d'habitat. Seules les populations de *Clethrionomys rutilus* démontraient des fluctuations importantes au cours d'une même année (de 3·ha⁻¹ à 37·ha⁻¹).

Mots clés: rongeurs, habitat, Alaska, populations, *Clethrionomys rutilus*, *Microtus oeconomus*, *M. gregalis*

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

Substantial information exists concerning population dynamics and ecology of arctic rodents (Batzli, 1975; Batzli *et al.*, 1980). Most data, however, are from the arctic coastal plain (Thompson, 1955; Pitelka, 1973; Martell and Pearson, 1978; Martell and Fuller, 1979). Little is known about the ecology and population dynamics of rodents in foothill or mountainous arctic tundra. Bee and Hall (1956) and Pruitt (1966) presented data on the ecology of rodents in foothill tundra but placed emphasis on rodents of the coastal plain. In this paper I discuss ecological distribution and short-term (two summers) population dynamics of rodents living in foothill tundra in northwestern Alaska.

Because of hilly and mountainous topography, the vegetation of the foothill tundra is more patchy than coastal tundra. This patchiness provides an opportunity to examine the effects of habitat on the structure of rodent communities and the response of populations of individual species to different habitat types. Besides describing ecological distribution, I assessed differences in several aspects (e.g. diversity, biomass, niche overlap) of small mammal communities among habitats. I also examined the specific hypothesis that populations of microtine rodents fluctuate in essentially the same manner in all habitats in which they occur (Krebs and Myers, 1974).

METHODS

The study was conducted in the De Long Mountains 160 km north of Kotzebue, Alaska. The De Long Mountains (68°07'N, 163°30'W) are located approximately 58 km inland from the Chukchi Sea and rise to between 610 m and 1190 m above mean sea level (asl). Most peaks, however, are less than 900 m asl. Most lowlands are dominated by cottongrass (*Eriophorum sp.*) and other sedges (*Carex spp.*), dwarf birches (*Betula spp.*), and willows (*Salix spp.*). Tall stands of riparian willows occur along most drainages. The higher elevations in the western De Long Mountains are dominated by *Dryas*, lichens, dwarf willows, and bare rock.

Trapping habitats were selected subjectively on the basis of dominant plant species and microtopography, and represented most of the major plant communities in the study area. One live-trapping grid was placed in each habitat type. I documented the vegetation by estimating the percent cover of mosses, lichens, grasses, sedges, shrubs, and total shrubs (ignoring overlap of species) on 15 trapping grids (Daubenmire, 1959). Nine quadrats were sampled on each column of each grid (a total of 36 on each of 14 grids, and 72 quadrats on one grid). Table 1 describes some of the physical and vegetative characteristics of the mammal sampling locations.

Fourteen grids, each consisting of 100 stations of one trap each, were trapped during 1978 and 1979. Grids were four

¹Montana College of Mineral Science and Technology, Butte, Montana 59701, U.S.A.

TABLE 1. Habitat characteristics of 15 live-trapping grids in the De Long Mountains, Alaska

	Bare ridge	Birch ridge	Birch flat	Shrubland	Sedge-willow ice scar	Sedge-willow meadow	Meadow (shrub)	Tussock 1	Tussock 2	Tussock 3	Meadow	Riparian grass-willow	Willow bar	Creek bottom 1	Creek bottom 2
Elevation (m)	274	320	198	279	282	229	259	206	152	206	270	150	190	244	274
Topography	Flat, sloping	Tussock, ice scars, sloping	Flat, level	Undulating, sloping	Large hummocks, ice scars	Flat, sloping	Flat, sloping	Tussocky, sloping	Tussocky, level	Tussocky, sloping	Flat, sloping	Flat, broken; spring	Gravelly creek channel	Eroding creek	Eroding creek
Mean depth to permafrost (cm)	49	37	45	47	47	32	36	33	34	35	32	35	—	43	—
Mean maximum height of veg. (cm)	14	22	72	69	55	88	36	33	27	28	28	69	22	49	84
% Coverage															
Bare ground	19	2	0	0	7	0	0	0	0	0	0	0	9	1	1
Litter	24	27	25	58	39	34	69	50	55	37	73	46	49	44	67
Lichen	40	22	21	8	19	2	9	2	9	3	0	0	6	2	8
Moss	27	37	69	63	54	43	80	39	35	70	80	77	52	63	73
Sedge	3	11	2	12	5	17	40	33	42	31	48	13	1	5	7
Grass	0	1	3	7	9	1	0	0	0	0	0	4	4	8	9
Herb	1	7	5	20	13	3	5	5	6	4	2	34	30	12	14
All shrubs	42	59	55	26	35	15	44	73	41	53	28	12	29	33	39
<i>Betula nana</i>	37	29	40	1	6	1	9	21	10	22	7	0	0	0	1
<i>Salix</i> sp.	1	4	5	25	20	13	27	6	2	0	16	12	19	32	34
<i>Ledum groenlandicum</i>	0	6	2	0	6	0	1	5	14	6	0	0	0	0	0
<i>Shepherdia canadensis</i>	0	0	0	0	2	0	0	0	0	0	0	1	8	0	0
<i>Empetrum nigrum</i>	0	1	0	0	3	0	0	3	2	8	0	0	0	0	1
<i>Vaccinium uliginosum</i>	2	10	1	1	11	0	2	3	3	1	5	1	0	0	2
<i>V. vitis-idaea</i>	1	12	6	1	0	1	4	5	16	15	0	0	0	0	10
<i>Andromeda polifolia</i>	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0

columns wide by 25 rows long and encompassed areas of 0.76 ha. During 1979, I added a grid containing 200 stations in eight columns and 25 rows (1.76 ha) in an upland shrub habitat. Columns on all grids were 15 m apart and rows were 7 m apart. Grids were sampled for three consecutive days each during June, July, and August 1978 and 1979.

Sherman live-traps (23 × 8 × 9 cm) were covered with plywood, baited with rolled oats and peanut butter, and checked once daily. Animals were individually numbered by toe-clipping and released at the point of capture. The number, location of capture, sex, breeding condition, and weight were recorded for each animal each time it was captured.

Population densities are expressed by the number of individuals captured per trapping grid and the number of individuals per hectare (number captured/area of grid). No attempt was made to estimate population density by capture-recapture techniques because of problems of nonrandom sampling (Krebs, 1977).

Biomass densities are represented by the sum of weights of individuals divided by the area occupied by each grid. Species diversity was measured by the Shannon-Weaver formula (Pielou, 1966); niche breadth was calculated according to Levins (1968); species association was calculated according to Dice (1945) (for comparisons with Pruitt's (1966) data); and niche overlap was calculated using Pianka's (1973) formula.

RESULTS AND DISCUSSION

Species Distribution

Numbers of small mammals trapped in various habitat types ranged from three (bare ridge) to 96 (riparian grass-willow) (Table 2). Two of the three tussock grids in the De Long Mountains had relatively high numbers of rodents but the third had very few animals. A shrub-covered location had relatively high numbers of rodents and the mat cushion type had low numbers of rodents. In contrast, Pruitt (1966), working on the coastal plain near the De Long Mountains, found that tussock habitats contained the largest number of small mammals whereas meadows and mat cushion areas contained intermediate numbers, and shrublands contained the smallest number.

The number of species in the various habitat types ranged from one (bare ridge) to six (riparian grass-willow and birch-tussock) with most habitats supporting four to five species of small mammals. The diversity indices were lowest (0) on the bare ridge and highest (1.54) in the riparian grass-willow. Pruitt (1966) found tussock areas to have the highest diversity and shrublands the lowest. In the De Long Mountains, tussock areas had lower small mammal diversities than shrublands.

The average monthly biomass was directly related to the number of individuals, with highest (340.3 g·ha⁻¹) occurring in the birch flat and the lowest (11.3 g·ha⁻¹) occurring on the

TABLE 2. Number of small mammals live-trapped on 15 grids in the De Long Mountains, Alaska, during 1978 and 1979¹

	Bare ridge	Birch ridge	Birch flat	Shrubland ²	Sedge-willow ice scar	Sedge-willow meadow	Meadow (shrub)	Tussock 1	Tussock 2	Tussock 3	Meadow	Periodically Flooded			Total number in all habitats	Number of habitats occupied	Niche breadth		
												Riparian grass-willow	Willow bar	Creek bottom 1				Creek bottom 2	
Northern red-backed voles	3	33	59	5	13	9	2	37	39	18	3	29	38	6	7	301	15	8.67	
Tundra voles	0	0	0	1	1	1	21	1	0	2	12	22	7	0	1	69	10	4.23	
Brown lemmings	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1.00	
Collared lemmings	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	
Singing voles	0	1	0	2	5	5	0	1	0	0	0	6	6	0	12	38	8	5.31	
Masked shrews	0	0	3	0	2	7	10	7	3	2	3	4	1	2	5	49	12	8.61	
Arctic shrews (<i>Sorex arcticus</i>)	0	0	1	0	0	1	7	1	4	0	6	6	0	0	0	26	7	4.83	
Dusky shrews	0	0	4	6	8	0	2	1	3	0	0	28	0	0	13	65	8	3.90	
Number of species	1	2	4	5	5	5	5	6	4	3	5	6	4	2	5				
Diversity index	0	0.13	0.48	1.33	1.32	1.33	1.28	0.80	0.73	0.60	1.33	1.54	0.82	0.56	1.40				
Average monthly biomass (g) 1978-1979	11.3	159.7	340.3	89.4	101.4	77.2	151.5	149.6	159.8	150.8	105.8	335.0	294.8	23.7	219.5				
Average change in biomass (g) June-August	22.2	202.6	620.3	225.9	124.1	42.1	119.0	227.8	203.6	129.1	165.9	277.6	335.6	23.7	171.5				
Change in biomass (g) August 1978-June 1979	-44.2	-301.4	-308.0	NA	-98.3	-118.8	-109.0	-419.6	-516.8	-279.1	-210.5	-462.0	-303.3	-62.4	-210.5				
Months that animals were present	1978	-JA	JJA	JJA	NA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA	JJA
	1979	---	JJA	JJA	JJA	-JA	JJA	JJA	-JA	J--	-JA	JJA	JJA	-JA	-A	-JA	-JA	-JA	-JA

¹Diversity = $\sum \frac{1}{n} \text{Pi log Pi}$; niche breadth = $1/\sum \text{Pi}^2$

²Grid larger than other grids. Numbers = $0.429 \times$ the actual number captured.

bare ridge habitat. The two-year average for all areas was $158.0 \text{ g}\cdot\text{ha}^{-1}$ which was lower than the three-year (1959-61) average in the Ogotruk drainage west of the De Long Mountains ($\bar{x} = 311.6 \text{ g}\cdot\text{ha}^{-1}$, range 91.4-934.1 $\text{g}\cdot\text{ha}^{-1}$; Pruitt, 1966).

Six habitats contained small mammals during all six sampling periods, and all contained animals during at least two of the six periods. Of those without continuous occupation by small mammals, all but one were vacant during June in one or both years. This may indicate that few, if any, animals were able to survive winter or spring flooding in those habitats. Tundra voles (*Microtus oeconomus*) apparently survived the winter in the sedge tussock habitat and were present in June 1979 but disappeared by August after a period of intense rain. That habitat was occupied in August by northern red-backed voles (*Clethrionomys rutilus*).

The number of habitats occupied by a species was not necessarily directly related to its abundance. Some of the least abundant species (e.g. masked shrew [*Sorex cinereus*]) were captured in more habitats than more abundant species (e.g. tundra vole). Northern red-backed voles were ubiquitous, and masked shrews and tundra voles occurred in most habitats.

Although all species were present in several habitats, none were present in equal densities in all habitats. Some species (e.g. dusky shrew [*Sorex vagrans*]) occurred in high densities in only one or two habitats with few individuals occurring in other habitats. The singing vole (*Microtus gregalis*), which occurred in the same number of habitats as the dusky shrew, was present in more uniform numbers among various habitats than the dusky shrew.

The niche breadth index accounts for both the number of habitats occupied and the evenness of occupation among habitats. In the De Long Mountains, northern red-backed voles had the broadest niche (Table 2). Pruitt (1966) also found northern red-backed voles to have broad habitat tolerance while tundra voles and brown lemmings had restricted habitat tolerances. Batzli and Jung (1980) did not find northern red-backed voles north of the Brooks Range, but found tundra voles in fewer habitats than brown or collared lemmings. However, the discrepancy in niche breadths of lemmings and tundra voles between Batzli and Jung's (1980) study area and the De Long Mountains cannot be fully assessed with the limited data (one capture each of brown and collared lemmings) from the De Long Mountains. Whitney (1976) compared tundra voles and northern red-backed voles in the boreal forest and also found that tundra voles occupied a more restricted niche than northern red-backed voles.

Temporal Relationships

Populations of microtine rodents were variable in the De Long Mountains; most populations remained below $10\cdot\text{ha}^{-1}$ whereas some reached densities over $30\cdot\text{ha}^{-1}$ (Fig. 1). The numbers and fluctuations were within the ranges recorded for these species in other studies.

Most population data for northern red-backed voles show that they undergo a regular seasonal population fluctuation, starting with low numbers in June and reaching high densities in August or September (Fuller, 1969; Whitney, 1976; Martell and Fuller, 1979). Densities in various studies ranged from

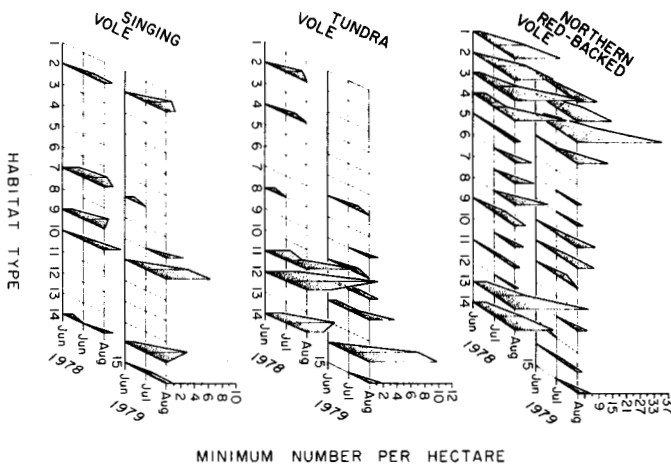


FIG. 1. Population densities of rodents on 15 live-trapping grids during 1978 and 1979 in the De Long Mountains, Alaska. Legend:

- | | | |
|----------------|--------------------------|---------------------|
| 1. Birch ridge | 6. Creek bottom 1 | 11. Meadow |
| 2. Willow bar | 7. Sedge-willow meadow | 12. Meadow shrub |
| 3. Birch flat | 8. Tussock 3 | 13. Tussock 2 |
| 4. Tussock 1 | 9. Sedge-willow ice scar | 14. Riparian-willow |
| 5. Bare ridge | 10. Creek bottom 2 | 15. Shrubland |

June populations of 2·ha⁻¹ to 32·ha⁻¹ (Fuller, 1969) to fall populations of 5·ha⁻¹ to 62·ha⁻¹ (Whitney, 1976). In most areas where this species has been studied, it also undergoes periodic fluctuations (Fuller, 1969); however, in some areas northern red-backed vole populations have been found to be relatively stable interannually (Whitney, 1976; Martell and Fuller, 1979). In the De Long Mountains northern red-backed voles undergo the typical seasonal fluctuation but it is not yet possible to determine the nature of long-term fluctuations.

Populations of tundra voles in the De Long Mountains were relatively low, as low as those described in the first three years of Batzli and Jung's (1980) study near Meade River. Batzli and Jung (1980) found that tundra vole population densities near Meade River remained relatively low (2-6·ha⁻¹) over a three-year period but increased the fourth year to 35·ha⁻¹. Whitney (1976) also found tundra vole populations to be quite variable. In Whitney's study area near Fairbanks, tundra voles reached population densities of 73-83·ha⁻¹ during the second year of study, rapidly declined the same year, and were no longer trappable by the third year.

During two summers, populations of brown lemmings in the De Long Mountains were very low. In other areas populations of this species fluctuate greatly or remain fairly stable. Brown lemming populations near Barrow characteristically have three- to six-year cycles with lows of approximately 0.02·ha⁻¹ and highs of up to 255·ha⁻¹ (Thompson, 1955; Pitelka, 1973; Batzli *et al.*, 1980). However, near Meade River, about 100 km south of Barrow, brown lemming populations remained relatively low (2-6·ha⁻¹) and stable over a four-year period (Batzli and Jung, 1980).

Densities of singing voles remained low in the De Long Mountains but were slightly higher during 1979 than during 1978. Pruitt (1966) found singing voles to be the second most common rodent occurring in the region west of the De Long Mountains. They were found in only one habitat (snow-bed

community). Numbers of singing voles captured in equal numbers of traps decreased from 51 animals in 1959 to one in 1961. This suggests that singing voles can undergo large fluctuations in numbers.

In summary, populations of three microtine rodents in the De Long Mountains during 1978 and 1979 occurred in densities similar to those found in other subarctic and arctic regions of North America. Northern red-backed voles underwent seasonal increases which are apparently typical for this species. Tundra voles and singing voles remained low throughout both summers. According to various studies, those species may or may not undergo "cycles" in population densities. Densities of brown lemmings and collared lemmings remained extremely low through both summers.

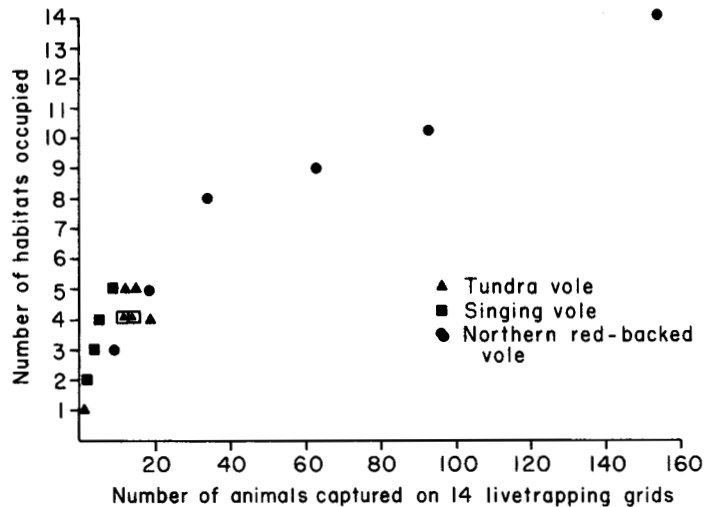


FIG. 2. Number of habitats occupied by rodents in relation to population density in the De Long Mountains, Alaska.

Seasonal Changes In Habitat Associations

Some effects of population increases on habitat associations are demonstrated in Figures 1 and 2. As northern red-backed vole populations increased each summer, they occupied more habitats ($r = 0.948$, $d.f. = 4$, $0.01 < P < 0.05$). However, within the small ranges of population densities of tundra and singing voles, tundra voles ($r = -0.151$, $d.f. = 4$, $P > 0.50$) and singing voles ($r = 0.725$, $d.f. = 4$, $0.05 < P < 0.10$) demonstrated no consistent relationship between population density and the number of habitats occupied.

Populations of rodents in the De Long Mountains vary both spatially and temporally (Fig. 1). I assumed that habitats occupied in June were those where animals survived the winter and were, therefore, most important to the species. Rodents demonstrated distinct segregations in June with overlap in habitat occupation occurring only in 1978 in the riparian grass-willow. As the summer progressed and northern red-backed vole populations increased, habitat segregation became less distinct. By August, all habitats were occupied by either northern red-backed voles or by variously mixed populations of northern red-backed voles, tundra voles, and singing voles.

Because tundra vole and singing vole populations remained relatively low, most of the overlap in occupation of habitats was the result of northern red-backed voles invading new habitats as their numbers increased. Contrary to my results, Krebs and Wingate (1976) found that niche breadth did not increase as northern red-backed vole populations increased.

Little is known about invasions of new habitats by small microtine rodents. Krebs and Myers (1974), in a review of microtine population dynamics, described a general population syndrome in which emigration occurred during the increase phase of population cycles. The fate of emigrating animals was not known and the influence of habitat on emigrating animals was not discussed. However, populations of northern red-backed voles in the De Long Mountains seem to occupy additional marginal habitats as their populations increase, in a manner similar to muskrats (*Ondatra zibethicus*) (Errington, 1967) and arctic ground squirrels (*Spermophilus parryi*) (Carl, 1971).

TABLE 3. Comparison of overwintering habitats of three species of rodents in the De Long Mountains, Alaska¹

	F Value	Relative Habitat Values	
		High	Low
Permafrost (cm)	7.54	$\frac{Rv_3^2 Tv Sv Rv_1}{Rv_3 Sv Tv Rv_1}$	
Maximum height of veg. (cm)	22.94	$\frac{Rv_3 Sv Tv Rv_1}{Tv Sv Rv_1 Rv_3}$	
Litter (% cover)	23.24	$\frac{Rv_3 Sv Tv Rv_1}{Rv_3 Sv Tv Rv_1}$	
Shrubs > 50 cm	9.66	$\frac{Rv_3 Sv Tv Rv_1}{Rv_1 Rv_3 Tv Sv}$	
Lichen	14.34	$\frac{Rv_1 Rv_3 Tv Sv}{Rv_1 Rv_3 Tv Sv}$	
Moss	1.06 N.S.		
Sedge	39.84	$\frac{Tv Sv Rv_1 Rv_3}{Sv Rv_3 Rv_1 Tv}$	
Grass	8.05	$\frac{Sv Rv_3 Rv_1 Tv}{Sv Rv_1 Rv_3 Tv}$	
Herbs	27.96	$\frac{Sv Rv_1 Rv_3 Tv}{Sv Rv_1 Rv_3 Tv}$	
Shrubs < 0.5 m	1.90 N.S.		
Birch (<i>Betula nana</i>)	23.66	$\frac{Rv_1 Rv_3 Tv Sv}{Tv Rv_3 Sv Rv_1}$	
Willow (<i>Salix</i> sp.)	12.85	$\frac{Tv Rv_3 Sv Rv_1}{Tv Rv_3 Sv Rv_1}$	
Labrador tea (<i>Ledum groenlandicum</i>)	8.90	$\frac{Rv_1 Rv_3 Tv Sv}{Rv_1 Rv_3 Tv Sv}$	
Crowberry (<i>Empetrum nigrum</i>)	0.02 N.S.		
Lingonberry (<i>Vaccinium vitis-idaea</i>)	4.89	$\frac{Rv_1 Tv Sv Rv_3}{Rv_1 Rv_3 Tv Sv}$	
Blueberry (<i>V. uliginosum</i>)	7.32	$\frac{Rv_1 Rv_3 Tv Sv}{Rv_1 Rv_3 Tv Sv}$	

¹The Newman-Keuls test was used to compare among variables. A significance level of $P < 0.05$ was used.

²Habitats: Rv_1 = Northern red-backed vole, birch ridge
 Rv_3 = Northern red-backed vole, birch flat
 Tv = Tundra vole, meadow (shrub)
 Sv = Singing vole, riparian grass-willow

Eighteen habitat variables (Tables 1 and 3) were estimated and compared (Newman-Keuls Test [Zar, 1974]) to determine if habitats continuously or frequently occupied by each of the most commonly captured rodent species were distinct from those occupied by the other species. Northern red-backed voles continuously occupied two habitats (birch ridge and birch flat) and tundra voles continuously occupied one habitat (meadow shrub). Singing voles did not continuously occupy any of the habitats, but were trapped in the riparian grass-willow during all periods except July 1979.

The two habitats occupied by northern red-backed voles were dissimilar (Table 3). There were, however, consistent differences between each of the two northern red-backed vole habitats and those continuously occupied by tundra voles or singing voles. Habitats continuously occupied by northern red-backed voles consistently differed from those of tundra voles in having a lower percent cover of litter and willows and a higher percent cover of lichens, birch, and Labrador tea. Tundra vole habitat differed from singing vole habitat in having shorter maximum vegetation height, lower percent cover of grass, herbs, and crowberry, and higher percent cover of litter, lichen, birch, sedge, and low willow.

Consistent and significant differences among habitats occupied by each of the three species occurred only in the percent cover of litter, lichen, and birch. Both of the northern red-backed vole habitats also contained significantly less sedge cover than habitats occupied by tundra and singing voles. Tundra voles continuously occupied habitats with the highest percent cover of litter and sedges, as suggested by Getz (1961) and Grant (1971) for other *Microtus* spp., and singing voles occupied habitats with an intermediate but substantial accumulation of litter. Northern red-backed voles occupied habitats with sparse litter cover, and areas with high cover of birches and lichens. This is consistent with the occupation by northern red-backed voles of areas with high cover of birch and lichens in the Northwest Territories (Douglass, 1977) and by other *Clethrionomys* spp. elsewhere (Pollard and Relton, 1973). Percent cover of birch was intermediate in the tundra vole habitat and absent from the singing vole habitat.

Habitats continuously or most frequently occupied by northern red-backed voles, tundra voles, and singing voles apparently were segregated along a moisture gradient, with northern red-backed voles occurring in the driest habitats and tundra voles occurring in the wettest habitats. Litter, sedges, and willows tend to have higher cover values on poorly drained sites whereas lichens and birch generally have higher cover values on well-drained sites. Additional research, including an assessment of the role of rhizomatous vs. non-rhizomatous monocots, would be useful in clarifying habitat segregation among these rodents.

The presence of one species of small mammal may determine how other species use a given habitat (Morris, 1969; Grant, 1972; Douglass, 1976), may affect population dynamics of other species (Redfield *et al.*, 1977), or may have no effect at all (Grant, 1972; Krebs, 1977).

To obtain some insight into interactions among species of rodents in the De Long Mountains, I calculated (based on data from all grids) coefficients of association (CA) and niche overlap (O_{ij}) for the most abundant species (Table 4). A CA of less than 1.0 indicates that the two species occurred together less often than would be expected by chance. A CA value greater than 1.0 indicates that the two species occurred together more frequently than expected.

In the De Long Mountains during 1978 and 1979, northern red-backed voles occurred with tundra voles at the beginning of the summer less frequently than expected by chance, but not at the end of the summer (Table 4). This could indicate that

TABLE 4. Coefficients of association (CA) and niche overlap (O_{ij}) between pairs of species of voles in the De Long Mountains (1978 and 1979), and CA in the Ogotoruk region (1959-1961)¹

	Northern red-backed vole				Singing vole			
	Year	Month	CA	O_{ij}	Year	Month	CA	O_{ij}
Tundra vole	1978	June	0.70	0.200	1978	June	1.17	0.145
		July	1.17	0.335		July	0.70	0.441
		August	1.00	0.172		August	0.88	0.104
	1979	June	0.00	0.000	1979	June	0.00	0.000
		July	0.75	0.261		July	1.50	0.923
		August	0.90	0.419		August	1.60	0.133
Mean	1978-1979		0.75	0.231	1978-1979		0.96	0.291
Ogotoruk Region	1959-1961		1.44	—	1959-1961		0.00	—
Northern red-backed vole	1978	June			1978	June	0.93	0.246
		July				July	0.93	0.245
		August				August	1.00	0.383
	1979	June			1979	June	0.00	0.000
		July				July	0.94	0.309
		August				August	1.13	0.359
Mean	1978-1979				1978-1979		0.82	0.257
Ogotoruk Region	1959-1961				1959-1961		0.00	—

¹Coefficient of association = $CA = hn/ab$, where h = number of samples in which both species a and b occur, n = number of samples, a = number of samples in which species a occurs, and b = number of samples in which species b occurs. Data for 1959-1961 are from Pruitt (1966).

Niche overlap = $O_{ij} = \Sigma(x_{ik} x_{ij}) / \sqrt{\Sigma x_{ik}^2 \Sigma x_{jk}^2}$, where x_{ik} = proportion of species i in habitat k , and x_{jk} = proportion of j in habitat k .

some mild competitive exclusion was acting to separate the species in early summer, or that they had different habitat preferences. Singing voles did not show a consistent pattern of association with either of the other voles. Pruitt (1966), however, found that northern red-backed voles and tundra voles occurred together west of the De Long Mountains more frequently than expected, and singing voles were not captured with the other two species. Existing data are inadequate to explain the discrepancy in rodent species associations between the De Long Mountains and the coastal plain to the west.

The niche overlap calculations suggested that the three species of rodents occupied discrete niches (Table 4). In this study the niche overlap index measures the similarities of habitat niches; 0.0 indicates no similarity and 1.0 indicates similarity. Tundra voles and singing voles had the most similar niches ($O_{ij} = 0.923$) but only during July 1979. Even though northern red-backed voles occupied more habitats as their numbers increased, their habitat niche remained distinct from the other species ($O_{ij} < 0.5$). This is consistent with the analysis of specific habitat variables discussed above.

CONCLUSIONS

In this study I was interested in determining whether small mammal communities responded to habitat patchiness related to topography in foothill tundra. Several associations were evident. All habitats contained small mammals including rodents and insectivores, but most habitats were dominated by one to three species of microtine rodents. The most numerous species depended on type of habitat and the month in which the habitat was trapped. In early summer just after snowmelt, many habitats were not occupied and others were occupied only by

single species. During early summer northern red-backed voles, tundra voles, and singing voles occurred in separate habitats, apparently along a moisture gradient. As the summer progressed, segregation was not as obvious because northern red-backed voles eventually occupied all habitats.

I conclude that patchiness in foothill tundra was used by small mammals for habitat segregation and this segregation was most pronounced during the critical spring period (Fuller, 1969) when many habitat types were inundated by snowmelt or runoff. During this period the topography of the foothill tundra not only provided areas with different vegetation but also provided a variety of areas where rodents could escape the effects of melting snow.

I also was interested in determining if populations of microtine rodents fluctuated similarly in all habitats as suggested by Krebs and Myers (1974). At the densities that occurred in the De Long Mountains during 1978 and 1979, microtine rodent populations appeared not to fluctuate similarly among all habitats in which they occurred. This was particularly evident in the spring extinctions in many habitats described above. Most of the microtine rodents discussed by Krebs and Myers (1974) reached very high densities ($> 50 \cdot \text{ha}^{-1}$). If rodent populations in the De Long Mountains increase to such densities in the future, they may do so similarly in all habitats.

If future research is performed on ecological distribution of small mammals in foothill tundra, I would recommend investigating three aspects:

1. What specifically happens when northern red-backed vole populations increase and niche breadth broadens? This could be important to general population theory by providing insight into the fate of emigrating animals.
2. Do rodents respond directly to specific habitat variables as

suggested above or are these variables and the rodents responding to something else? This could be examined through more sophisticated descriptive research or by using an experimental approach.

3. What are the long-term relationships between populations of rodents in foothill tundra vs. those previously described in coastal tundra? This could be discovered only with long-term (~ 10-year) population monitoring.

ACKNOWLEDGEMENTS

Data for this paper were collected while field studies were being conducted for GCO Minerals Co. I would like to express my appreciation to D. Kennedy, J. Britton, and J. Fernette for making this study possible. I also would like to thank D. Hollingsdale for assistance with drafting and D. Yokel for assistance in the field. Finally, I extend my appreciation to G.O. Batzli and A.M. Martell for their helpful suggestions on an earlier draft.

REFERENCES

- BATZLI, G.O. 1975. The role of small mammals in arctic ecosystems. In: Golly, F.B., Petruszewicz, K. and Ryzkowski, L. (eds.). *Small Mammals: Their Productivity and Population Dynamics*. Cambridge, England. Cambridge University Press. 243-268.
- _____ and JUNG, H.J.G. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. *Arctic and Alpine Research* 12:483-499.
- BATZLI, G.O., WHITE, R.G., MacLEAN, S.F., Jr., PITELKA, F.A. and COLLIER, B.C. 1980. The herbivore-based trophic system. In: Brown, J., Miller, P.C., Tieszen, L. and Bunnell, F. (eds.). *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*. International Biological Programme 12. Cambridge: Cambridge University Press. 571 p.
- BEE, J.W. and HALL, E.R. 1956. *Mammals of Northern Alaska*. University of Kansas Museum of Natural History, Miscellaneous Publication No. 8. Lawrence, Kansas: Allen Press. 309 p.
- CARL, E.A. 1971. Population control in arctic ground squirrels. *Ecology* 52:395-413.
- DAUBENMIRE, R.F. 1959. A canopy coverage method of vegetation analysis. *Northwest Science* 33:43-64.
- DICE, L.R. 1945. Measures of the amount of ecological associations between species. *Ecology* 26:196-302.
- DOUGLASS, R.J. 1976. Spatial interactions and micro-habitat selection of two sympatric voles, *Microtus montanus* and *M. pennsylvanicus*. *Ecology* 57:346-352.
- _____. 1977. Effects of winter roads on small mammals. *Journal of Applied Ecology* 14:827-834.
- ERRINGTON, P.L. 1967. *Of Predation and Life*. Ames, Iowa: Iowa State University Press. 277 p.
- FULLER, W.A. 1969. Changes in numbers of three species of small rodents near Great Slave Lake, N.W.T., Canada, 1964-1967, and their significance for general population theory. *Annaler Zoologica Fennica* 6:113-144.
- GETZ, L.L. 1961. Factors influencing the local distribution of *Microtus* and *Synaptomys* in southern Michigan. *Ecology* 42:110-119.
- GRANT, P.R. 1971. The habitat preference of *Microtus pennsylvanicus* and its relevance to the distribution of this species on an island. *Journal of Mammalogy* 52:351-361.
- _____. 1972. Interspecific competition among rodents. *Annual Review of Ecology and Systematics* 3:79-106.
- KREBS, C.J. 1977. Competition between *Microtus pennsylvanicus* and *Microtus ochrogaster*. *American Midland Naturalist* 97:42-49.
- _____ and MYERS, J.H. 1974. Population cycles in small mammals. *Advances in Ecological Research* 8:267-399.
- KREBS, C.J. and WINGATE, I. 1976. Small mammal communities of the Kluane region, Yukon Territory. *Canadian Field-Naturalist* 90:379-389.
- LEVINS, R. 1968. *Evolution in changing environments: Some theoretical explorations*. Princeton, NJ: Princeton University Press. 120 p.
- MARTELL, A.M. and FULLER, W.A. 1979. Comparative demography of *Clethrionomys rutilus* in taiga and tundra in the low Arctic. *Canadian Journal of Zoology* 57:2106-2120.
- MARTELL, A.M. and PEARSON, A.M. 1978. The small mammals of the Mackenzie Delta Region, Northwest Territories, Canada. *Arctic* 31:475-488.
- MORRIS, R.D. 1969. Competitive exclusion between *Microtus* and *Clethrionomys* in the aspen parkland of Saskatchewan. *Journal of Mammalogy* 50:291-301.
- PIANKA, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53-74.
- PIELOU, E.E. 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 7:549-557.
- PITELKA, F.A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. In: Gunn, W.W.H. (ed.). *NARL Twenty-fifth Anniversary Symposium*. Washington, D.C.: The Arctic Institute of North America. 199-215.
- POLLARD, E. and RELTON, J.H. 1973. A study of small mammals in hedges and cultivated fields. *Journal of Applied Ecology* 7:549-557.
- PRUITT, W.O., Jr. 1966. Ecology of terrestrial mammals. In: Wilimovsky, J.H. and Wolf, J.N. (eds.). *Environment of the Cape Thompson Region, Alaska*. Washington, D.C.: U.S. Atomic Energy Commission. 519-564.
- REDFIELD, J.A., KREBS, C.J. and TAIT, M.J. 1977. Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal British Columbia. *Journal of Animal Ecology* 46:607-616.
- THOMPSON, D.Q. 1955. The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. *Transactions of the North American Wildlife Conference* 20:166-176.
- WHITNEY, P. 1976. Population ecology of two sympatric species of sub-arctic microtine rodents. *Ecological Monographs* 46:85-104.
- ZAR, J.H. 1974. *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall. 620 p.