

Habitat use by singing voles and tundra voles in the southern Yukon

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Summary. We investigated how far competitive interactions influence the use of habitats and relative abundance of two species of *Microtus* in the southwestern Yukon. We worked in the ecotone between alpine tundra and subalpine shrub tundra where populations of singing voles (*Microtus miurus*) and tundra voles (*M. oeconomus*) overlap little.

We removed tundra voles from shrub tundra on one live-trapping area to look at the effect on the contiguous population of singing voles in alpine tundra. The removal of tundra voles did not affect the distribution or relative abundance of singing voles. The spatial distribution of these species and their movements within habitats suggest that they have a strong habitat preference.

Populations of small mammals in the area are extremely dynamic and the relative importance of competitive interactions may change as density varies. At present we have no evidence that competition affects habitat use in *M. miurus*.

In areas where prairie voles (*Microtus ochrogaster*) and montane voles (*Microtus montanus*) are absent, meadow voles (*M. pennsylvanicus*) occupy a wider range of habitats (Findley 1954). This early observation, consistent with the emerging view of the importance of interspecific competition in natural communities, led Findley (1954) to suggest that competition among closely related microtines (Arvicolidae) was at least partly responsible for such distributional patterns. Since then, a number of studies, some on pairs of microtine species, have been undertaken to look into the role that interspecific interactions play influencing the distribution and abundance of these species (Grant 1972a, 1978). The morphologic and dietary similarities among microtines make them potential candidates for a strong competitive interaction.

A number of microtine species use habitats similarly. Many species occupy contiguous areas along well-defined ecotones between structurally different habitats (Koplin and Hoffman 1968; Guthrie 1971; Stoecker 1972; Iverson and Turner 1972; Morris and Grant 1972; Turner et al. 1975; Hawes 1976; Randall 1978). However, while most studies have suggested that competition for space mediated through aggressive behavior is responsible for the distributional pattern, the evidence has been unconvincing. Fur-

thermore, other studies have found no negative effects among pairs of species (Hawes 1976; Krebs 1977) or have suggested that in some areas habitat preferences may be sufficient to explain the patterns documented (Douglass 1976).

We studied two morphologically similar species of microtines: tundra voles and singing voles. Tundra voles (*Microtus oeconomus*) occur in moist tundra areas, sedge and cottongrass marshes (Banfield 1974; Youngman 1975). In the area of study they have been found in alpine and subalpine tundra and marshes as well as in spruce forest (Krebs and Wingate 1976). Singing voles (*M. miurus*), on the other hand, are mainly confined to alpine tundra (Banfield 1974; Youngman 1975) but have also been recorded at subalpine tundra, marshes and spruce forest (Krebs and Wingate 1976).

During 1981, we studied the habitat use by these species and tested experimentally the hypothesis that competitive interactions influence their habitat distribution and relative abundance. If interspecific interactions actively influence the spatial distribution of these species, the hypothesis predicts that removal of one species will result in a habitat change and density increase by the other species.

Study area

The field work was carried out during the snowfree season from April to September 1981, in the Kluane Ranges, 7 kilometers south of the south corner of Kluane Lake, Yukon (61 N, 138 W). We worked in two vegetation zones: alpine tundra and subalpine shrub tundra (Hoefs et al. 1975), which we considered to be different habitats.

Alpine tundra occupies the mountain tops above approximately 1500 m. Dwarfed vascular plants, moss and lichens dominate this community. Shrubs are very scarce or completely absent. Some of the common plant species are heather (*Cassiope*), dwarf willow (*Salix spp.*), arctic lupine (*Lupinus*), blueberry (*Vaccinium*), bearberry (*Arctostaphylos*), dwarf birch (*Betula*) and a variety of sedges and grasses.

Below the alpine tundra and above the treeline, from 1100 to 1500 m, the subalpine shrub tundra forms a broad belt characterized by tall shrubs (up to 3 m), mostly willow (*Salix glauca* and *S. reticulata*) and dwarf birch (*Betula glandulosa*). In some areas the cover is very dense, forming impenetrable thickets. Vascular plants such as heather (*Cassiope*) and grasses (*Festuca*) are common in the understory.

Methods

Habitat use patterns

We used snap-trap lines to determine where the species live and how abundant they are. These lines consisted of 20 stations spaced at 10 m intervals with three 'museum special' traps per station (Krebs 1964; Krebs and Wingate 1976). The traps were baited with peanut butter and were left in position for two days. Lines were trapped throughout the summer.

Live-trapping technique

We set two long, rectangular live-trapping grids: a control and an experimental. Each occupied nearly 1 ha with 102 'Longworth' live-traps arranged in a 6 × 17 grid. The distance between traps was 10 m. The grids were located at the ecotone between alpine tundra and subalpine shrub tundra, with approximately half the traps in each habitat. The grids were set perpendicular to each other. The closest traps between grids were 40 m (129 ft) apart. We set the traps for two nights every second week and left them locked open between trap sessions to allow voles to move in and out freely. The traps were provided with whole oats (as bait) and cotton batting (as bedding). All animals captured for the first time were ear-tagged with numbered fingerling fish tags. Every trap session we recorded: species, tag number, sex, breeding condition, weight and trap location. The breeding condition of individuals was assessed in the following way: for males the position of their testes was recorded as either scrotal (breeding) or abdominal (not breeding). For females we recorded if their vagina was perforate or not, nipple size (small, medium, large), pubic symphysis condition (open, slightly open, closed) and evident pregnancies.

Experimental manipulation

From the experimental grid we removed all tundra voles every trap session, starting in the second one (June 29) and continuing throughout the summer. The aim of the removal experiment was to reduce the population of tundra voles and keep the shrubby habitat vacant for the adjacent population of singing voles.

On the live-trapping grids we estimated the proportion of shrub cover (*Salix glauca*) within a circle of 6 m diameter centred around each trap station. Two perpendicular diameters were used in each circle to estimate cover by the line-intercept method (Mueller-Dumbois and Ellenberg 1974). We classified stations under five categories of shrub cover: 100%, 75%, 50%, 25% and 0%.

We used simple measures of niche breadth and niche overlap (Levins 1968; Colwell and Futuyama 1971; Southwood 1978; formulas 13.30 and 13.31 p445 and p446) to compare the spatial distribution between experimental and control areas.

We used both Cole's (C7) and Hurlbert's (C8) coefficients of interspecific association to indicate the strength of the associations. Both range from -1 when there is a strong negative association to +1 when the association is strongly positive (Cole 1949; Hurlbert 1969; Ratliff 1982).

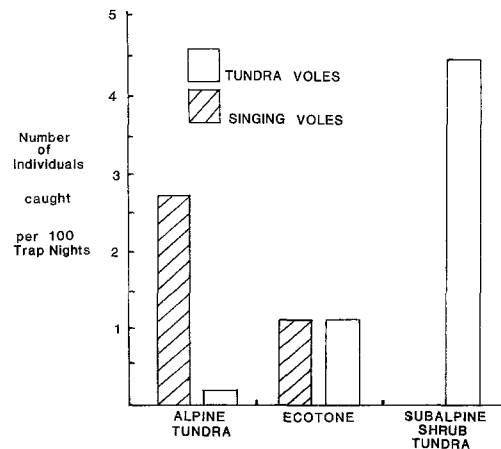


Fig. 1. Density indices for singing and tundra voles in different habitats for May to August 1981

Table 1. Resource matrix (number of individuals per trap-night times 1000), habitat niche breadth and habitat overlap for both species of voles using snap-traps. (Based on 15 singing voles and 27 tundra voles during 1200 trap-nights)

Species	Resource states			
	Alpine tundra	Ecotone	Subalpine shrub tundra	
Singing vole	27.08	11.11	0.0	38.19
Tundra vole	2.08	11.11	44.44	57.63
	29.16	22.22	44.44	95.82
Habitat niche breadth:				
	Singing vole		1.70	
	Tundra vole		1.58	
Actual habitat niche overlap (postcompetitive): $c = 0.23$				

Results

Patterns of habitat use

The ecotone between alpine tundra and subalpine shrub tundra is not sharply defined. It is characterized by a mosaic of shrub and open meadow patches where singing voles and tundra voles show a remarkably small overlap in their habitat use. Captures from the snap-trap lines in these two habitats show that singing voles occur mainly in the open meadows of the alpine tundra, but are also caught at the ecotone with the adjacent shrubby habitat (Fig. 1). From a total of 15 animals caught in 1200 trap-nights, 13 (87%) were in the open meadows while the remaining 2 (13%) were trapped in the ecotone between both habitats. No singing voles were caught in the subalpine shrub tundra.

Conversely, tundra voles occur mainly in the densely covered shrub tundra where 24 (89%) were caught. Of the remainder, 2 (7%) were in the ecotone while one individual (4%) was caught in the alpine tundra. The resource matrix for the snap-trap data indicates that these species have similar habitat niche breadths and that their habitat niche overlap is small (Table 1).

A more detailed view of the microhabitat distribution of both species at the ecotone is provided by the analysis

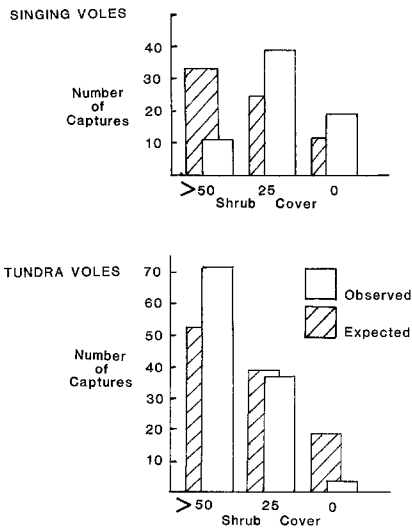


Fig. 2. Microhabitat use by singing voles and tundra voles on the control grid. Singing voles use open areas while tundra voles use areas with higher shrub cover. The expected value is obtained by assigning the captures proportionally to the number of traps in each shrub category

Table 2. Resource matrix (number of captures per trap-night times 1000), niche breadth and niche overlap for both species of voles on control grid for all summer

Species	Resource states: shrub cover categories					
	0	25	50	75	100	
Singing vole	53.22	51.58	12.82	8.65	0.0	126.27
Tundra vole	8.40	47.61	64.10	73.59	95.23	288.93
	61.62	99.19	76.92	82.24	95.23	415.20
Habitat niche breadth						
	Singing vole		2.78			
	Tundra vole		3.97			
Actual habitat niche overlap (postcompetitive) $c=0.36$						

of frequency of captures at live-traps under different cover conditions on the control grid (Fig. 2).

Singing voles were captured more frequently at live-trap stations surrounded by little (25%) or no shrub cover ($G_{adj.} = 32.28$, $df. 2$, $P < 0.01$). Few animals were caught at trap stations under more than 50% shrub cover. Tundra voles also differed in their habitat use significantly from random ($G_{adj.} = 25.55$, $df. 2$, $P < 0.01$) but in the opposite direction. They mostly used traps with high shrub cover and avoided traps in open habitat. Tundra voles use a higher number of microhabitats than singing voles on the control grid. The actual microhabitat niche overlap (postcompetitive) is larger than the habitat overlap but the difference is relatively small (Table 2).

There were more traps used exclusively by either of the two species than traps shared by both. Throughout the summer 23 individual singing voles and 33 individual tundra voles were caught on the control grid a total of 69 and 110 times, respectively, over 2142 trap-nights. From a total of 102 trap stations, 20 were used only by singing voles, 39 were used only by tundra voles, 6 by both species and

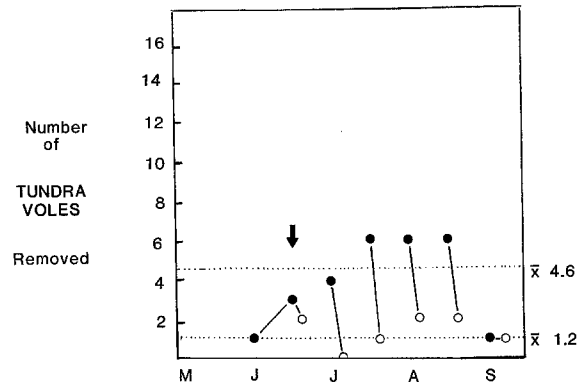


Fig. 3. Number of tundra voles removed. The average number of individuals removed declined within trap sessions. Closed circles indicate the first night and open circles indicate the second night. Arrow represents the beginning of the manipulation

the rest were not used. The species are negatively associated ($X^2 = 5.17$, $P < 0.05$) and the strength of the association is moderate ($C7 = -0.47$, $C8 = -0.47$). There were no trap saturation problems. Even when numbers were highest in both species, only 32% of the traps were used.

Removal experiment

A total of 35 tundra voles was removed throughout the summer from the experimental grid. After the removal of what we considered the resident population, an average of 5.8 tundra voles per session was caught (Fig. 3). Between the first and second night of each trap session the average number of animals caught and removed declined from 4.6 to 1.2. This reduction plus the fact that they were untagged individuals, indicates that the grid was almost free of tundra voles by the end of every session. Animals caught subsequently were dispersers from elsewhere. The removal resulted in a reduction of habitat use by tundra voles of at least 70% (estimated from the number of captures compared with that on the control).

Spatial distribution

If tundra voles actively influence the spatial distribution of singing voles, then the removal of the former will result in the use of subalpine shrub tundra (niche shift; ecological release) by singing voles. This ecological release would be reflected in any of the following ways. First, an increase in the number of traps shared by both species, due to the use of traps by singing voles of those sites from which tundra voles had been removed. Second, an increase in the frequency of captures of singing voles in those traps formerly used by tundra voles. Third, a shift in the kind of trap station used from open sites to trap stations under higher shrub cover. As a consequence of this shift both microhabitat niche breadth and overlap should be larger in the absence of the suspected competitor (virtual or pre-competitive niche breadth).

Were more traps shared by both species on the experimental grid? On the experimental grid 24 singing voles and 35 tundra voles were caught a total of 59 and 35 times respectively over 2142 trap nights. From a total of 102 traps, 20 were used by *Microtus miurus* alone, 20 by *Microtus oeconomus* alone and only 3 by both species. The rest of the traps were not used. Fisher's exact test did not reject

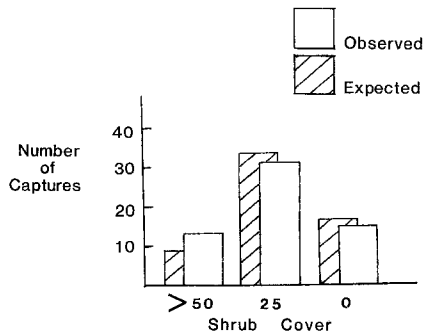


Fig. 4. Microhabitat use by singing voles on experimental grid. The use of shrub categories by singing voles is similar in both grids regardless of the absence of tundra voles. Expected values were obtained by assigning captures proportionally to the distribution in the control grid

Table 3. Resource matrix (number of captures per trap-night times 1000), niche breadth and niche overlap for both species of voles on experimental grid for all summer

Species	Resource states: shrub cover categories					
	0	25	50	75	100	
Singing vole	27.47	35.14	25.79	0.0	0.0	88.40
Tundra vole	9.15	7.93	19.84	61.90	0.0	98.82
	36.12	43.07	45.63	61.90	0.0	187.22
Habitat niche breadth						
	Singing vole		2.94			
	Tundra vole		2.23			
Virtual habitat niche overlap (precompetitive) $c=0.37$						

the hypothesis of independence ($P=0.34$). The coefficients of association give a moderate negative association ($C7=-0.42$, $C8=-0.42$). More traps were used by both species on the control grid. But in fact the number of traps used by *Microtus miurus* alone and shared with *Microtus oeconomus* is not significantly different between experimental and control grids ($G_{adj.}=1.42$, $df.1$, $P>0.10$).

Did singing voles more frequently use traps from which tundra voles had been removed? Singing voles were caught 54 times in traps used exclusively by them and 5 times in shared traps. Their frequency of captures at shared traps is lower in the experimental grid than in the control ($G_{adj.}=6.17$, $df.1$, $P<0.02$), and not higher as was predicted.

Did singing voles increase their use of the microhabitat from which tundra voles had been removed? According to the shrub categories used, the proportion of singing vole captures after the removal is not different from that on the control grid ($G_{adj.}=1.51$, $df.2$, $P>0.30$) (Fig. 4). A comparison of the actual (control) and virtual (experimental) microhabitat niche breadth of singing voles shows almost no difference between them. Accordingly, actual and virtual microhabitat overlap are strikingly similar (Table 3).

In summary, the removal of tundra voles had no effect on the spatial distribution of singing voles.

Movements between grids

A few individuals of both species were caught on both grids. Members of each species moved to the area in the new

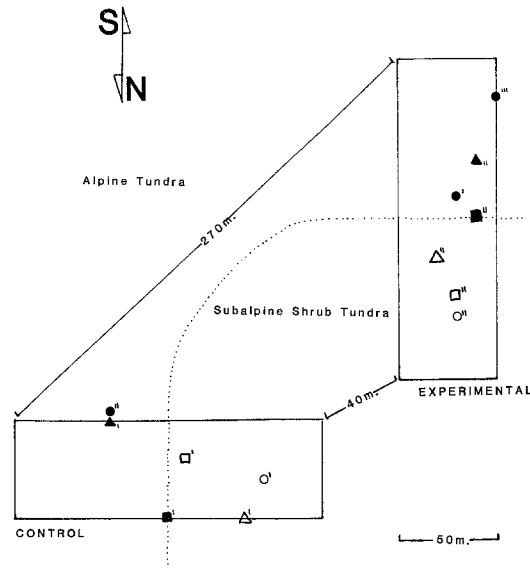


Fig. 5. Movements between grids. Closed figures represent singing voles and empty figures represent tundra voles. The subindices indicate the sequence of captures. Both species move between grids to their corresponding habitats

grid with a similar habitat to that from which they came. Such areas involved a greater distance to travel than that required to move to a different habitat on the same grid. This is more apparent in the movements of singing voles, since the areas of alpine tundra between the grids were farther apart. In alpine tundra the closest distance between traps in different grids was 150 m (485 ft).

Three singing voles travelled between grids. Two adult females moved from the control grid to the experimental grid, a distance of 230 m (744 ft) and 220 m (712 ft). An adult male moved from the experimental to the control grid and back, travelling 210 m (680 ft) and 260 m (841 ft). The trip back was done overnight (Fig. 5). The movements were recorded during June and early July, and by mid-July these individuals had disappeared from both grids.

Similarly, three tundra voles moved from the control grid to the experimental grid, where they were removed. Two adult females and an adult male travelled 130 m (421 ft), 160 m (518 ft) and 170 m (550 ft) respectively. The trip by the male was done overnight. These movements were recorded during June (Fig. 5).

Movements within grids

On the control grid tundra voles occupied two different areas, the west half (Rows 9 to 17) and a small part of the east corner (Rows 1 to 4). Trap stations in these areas had high shrub cover. They were absent from the open meadows area between these two which was occupied by singing voles. In spite of the relatively small distance between the areas (50 m), none of the tundra voles caught in one area were caught in the other area. This distance between shrub habitat patches is relatively small when compared with: a) the distance between the most widely separated capture points of individuals within each area (10 to 80 m) and b) the distances travelled by individuals from grid to grid within the same subalpine shrub tundra habitat (greater than 130 m).

Therefore, both species can move to the adjacent habi-

tat, since the movements normally recorded are far larger than the distance required to get to the contiguous habitat.

Population dynamics

Two or more species compete if an increase in any one results in a corresponding decrease in the others (MacArthur 1972). Even when the predictions from this definition do not discriminate other interactions from competition (predation, parasitism), it is useful to analyze the effect of one species on another. If one of these species has a negative effect (exploitation, interference) on the second, removal of tundra voles should result in an increase in numbers of singing voles. The increase would be produced either by higher reproductive rate, lower mortality, higher immigration, lower emigration, or a combination of these parameters. However, since singing voles did not utilize the area vacated by tundra voles, there should be no differences in their demographic parameters between grids. In fact, the following analysis shows that the populations were remarkably similar.

Numbers

Is the population of singing voles higher in the absence of a contiguous population of tundra voles? On the control grid the population of overwintered singing voles began at a very low density during June. The onset of breeding was not documented, as some females were already pregnant when trapping began. The first juveniles were trapped during the second week of July. From then on, the population increased continuously until the first week of September, reaching 37 individuals per hectare when the trapping ended. Throughout the summer a total of 23 individuals was caught; 8 adults (6 females and 2 males) and 15 juveniles (10 females and 5 males).

The singing vole population was also very low on the removal grid during June. With the recruitment of juveniles through July, they increased at a faster rate than on the control. Nevertheless, they remained at a lower level than on the control during August and September. A total of 21 individuals was caught with similar sex and age ratios to those of the control population: 8 adults (5 females and 3 males) and 13 juveniles (8 females and 5 males).

A comparison of the minimum number of animals known to be alive on both grids (Fig. 6) shows that the population of singing voles on the control grid increased to a higher level than that on the removal grid. This is contrary to what would be expected if tundra voles were having a negative influence on singing voles.

The total number of singing voles caught throughout the summer is very similar on both grids ($G_{adj.} = 0.08$, $P > 0.70$) as are the age and sex ratios ($G_{adj.} = 0.28$, $df. 2$, $P > 0.50$). The adult classes were pooled to obtain a joint class with an expected frequency greater than 5. There was a bias in the sex ratio towards females on both grids. On the control grid 75% of the adults and 66% of the juveniles were females. On the experimental grid 62% of the adults and 61% of the juveniles were females.

Reproduction

There are no evident differences in singing vole reproduction between grids. Females were already pregnant by the first trapping session on both grids. On both experimental

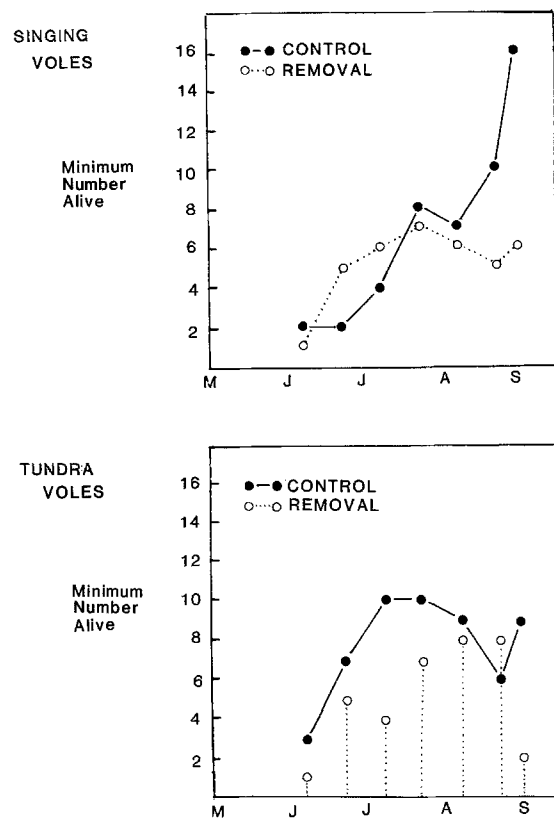


Fig. 6. Changes in minimum number alive for both singing and tundra voles on the experimental and control grids. Singing voles reached a higher density on the control grid

and control grids the first juveniles were caught in the second week of July. Therefore the onset of breeding was synchronous. There seemed to be two litters during the breeding season of 1981, the first born in mid-June and the second in mid-July.

On both grids half of the tagged adult females were caught only once or twice during June and early July and disappeared for the rest of the summer. We considered them transient individuals. Because the rest were caught in 3 to 5 trapping sessions we considered them residents. Following the breeding condition of the individual resident females, we estimated a minimum of 3 litters was produced on each grid. The number of juveniles recruited during July and August per adult female for the control and experimental grids was 2.5 and 2.6 respectively, or 5 and 6.5 when only the resident females are taken into account.

Discussion

Recent reviews have attempted to assess the role of competition by looking at the experimental evidence across diverse taxa (Schoener 1983; Connell 1983). In the following discussion we will concentrate on studies carried out with microtines (Arvicolidae) in an attempt to look for patterns in a more homogeneous subset.

A number of factors may influence the distribution of these two microtine species. While the well-defined pattern of non-overlapping populations could result from interference competition (Guthrie 1971), the structural difference of the vegetation from open meadows to a dense cover

of shrubs affects many other biotic and abiotic components of the community. The results from this study do not support the hypothesis that the habitat distribution of singing voles is influenced by competitive interactions. The use of trap stations indicated that both species showed a strong inverse distributional pattern in relation to habitat structure (shrub cover), but the removal of one species did not affect the distribution of the other. The resource matrix analysis supports this result. If competitive interactions were influencing the spatial distribution of singing voles, then the habitat niche breadth of this species should be larger in the absence of tundra voles. Similarly, virtual niche overlap should be larger than actual niche overlap. None of these predictions were supported. Both the habitat niche breadth and overlap of singing voles are very similar regardless of the removal of tundra voles. Furthermore, individuals of both species moved large distances within and between grids. This clearly shows that they could have moved to the adjacent habitat. Nevertheless, they were never caught there.

Several studies have dealt with habitat separation and interspecific interactions among microtines. Koplín and Hoffmann (1968) experimentally tested the hypothesis that habitat segregation of meadow voles (*M. pennsylvanicus*) and montane voles (*M. montanus*) is maintained by interspecific interactions. Montane voles made exploratory movements into the grassland after the removal of meadow voles. However, the experiment was criticized since the experimental plot was fenced and not grazed by bison, and had a 4 to 5 times higher density than the control (Grant 1972; Connell 1975; Birch 1979). The differences in habitat use by montane voles in experimental and control plots may have been a consequence of the different population densities and not of the absence of meadow voles. Stoecker (1972) did the inverse experiment of removing montane voles and found that meadow voles used the drier habitat in the absence of the former species. Neither studies were able to determine whether individuals that moved into the vacated areas remained there or were merely transients. Both studies lacked replicates and adequate controls. The studies suggested behavioral interactions as a mechanism for the habitat segregation.

Competitive interactions have also been invoked to explain habitat segregation among other pairs of related species. A number of distributional studies have suggested that active interference results in habitat segregation by red-backed voles (*Clethrionomys*) and meadow voles (*Microtus*) (Morris 1969; Grant 1972). The former live in woodlands and the latter in adjacent grasslands (Morris 1969). Experiments inside enclosures showed that *Clethrionomys* occurred more often in the grassland in the absence of *Microtus* (Grant 1969) and that *Microtus* occurred more often in the forest in the absence of *Clethrionomys* (Morris and Grant 1972). Both colonization of grassland habitat by red-backed voles and of spruce forest by meadow voles have been documented (Iverson and Turner 1972; Turner et al. 1975). In both cases the colonization took place during winter, once the breeding season was over, and animals disappeared from the colonized habitat at the onset of breeding. The authors suggested that the decrease in intraspecific aggression during the non-breeding season permitted these species to coexist. However their conclusion is based on a correlation. No experiment was done to confirm a causal relationship.

Hawes (1976) showed that *Microtus oregoni* was more restricted in its habitat use after the introduction of *M. townsendii*. However, in the same study the removal of *M. oregoni* did not influence habitat utilization by *M. longicaudus*. Similarly, Krebs (1977) found no evidence of negative demographic effects between *Microtus pennsylvanicus* and *M. ochrogaster* living in the same grassland areas.

Alternatively, there is support for the hypothesis that habitat segregation in microtines is related to habitat preferences. Differences in use of habitats related to physiological tolerances have been documented for some species. Montane voles are often found in drier places (even shrub-steppe communities) while meadow voles occupy more mesic habitats (Murie 1971; Banfield 1974). Water balance in meadow voles is not well adapted for dry situations (Getz 1963). Douglass (1976) demonstrated that these species show different habitat preferences and concluded that such preferences are probably the most important factor responsible for their segregation. He suggested that the relative importance of social interactions and habitat preferences may change along a gradient of habitats. At one extreme, when habitats are sharply defined, the distribution will be the result of habitat preferences, whereas if the habitat is uniform behavioral interactions may have a stronger influence.

In addition, habitats may become more similar not only because of the resemblance of their structural characteristics but because of the effect of population density. As the density of a species in a habitat increases, its suitability will decrease, reducing its difference from less suitable habitats (Fretwell and Lucas 1970; Merkt 1981). If populations of singing voles and tundra voles fluctuate, their interspecific interactions may be contingent on density changes. Cycles in populations of tundra voles have been documented in Finland and Alaska (Taitt and Krebs 1985). In the latter locality peak densities reached approximately 70 to 80 voles per hectare. While there have been no studies on the demography of singing voles, Krebs and Wingate (1976) reported changes in their abundance from year to year. Furthermore, the total disappearance of both species from the study site during the winter of 1981 indicates that they do fluctuate in the area. At present, however, neither species has been found in the area in higher numbers than those reported here (Krebs and Wingate 1976), and therefore densities may rarely be high enough for competitive interactions to occur.

Acknowledgements. We thank the Natural Sciences and Engineering Research Council of Canada, Consejo Nacional de Ciencia y Tecnología de Mexico, the Arctic Institute of North America and the Department of Indian Affairs and Northern Development for financial support. We thank Margriet De Poorter, Stan Boutin, Scott Gilbert and Jean Carey for their field assistance and an anonymous reviewer for suggestions.

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Received November 5, 1984