Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles

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In this study we investigated the influence of competitive interactions on the use of habitats and relative abundance of deer mice (*Peromyscus maniculatus*). If interspecific competition is influencing the habitat use and relative abundance of deer mice, then removal or introduction of potential competitors will change habitat use and abundance of this species. During the first field season we removed meadow voles (*Microtus pennsylvanicus*) to look at the effect on the contiguous population of deer mouse. The removal of one species had no effect on the other species' distribution or demography. In the second field season, meadow voles declined to very low numbers and we used their natural fluctuation as a removal experiment. Deer mouse populations were not affected even when the natural decline of meadow voles was more effective in maintaining the sedge meadow free of voles than the previous removal manipulation was. During the 3rd year, meadow voles colonized two areas of forest where deer mice had been alone the previous two field seasons. Red-backed voles (*Clethrionomys rutilus*), in turn, increased from very low numbers in four grids. Neither meadow voles nor red-backed voles affected the spatial distribution or abundance of deer mice. The results of this study indicate that competitive interactions have no influence on the use of habitats and relative abundance of the common species of small mammals in the southwestern Yukon.

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L'influence des interactions compétitives sur l'utilisation de l'habitat et sur l'abondance relative des souris sylvestres (*Peromyscus maniculatus*) a fait l'objet d'une étude. Si la compétition interspécifique a une influence sur ces paramètres, le retrait ou l'introduction de compétiteurs potentiels devrait entraîner des changements dans l'utilisation de l'habitat et la densité de la population. Au cours de la première saison d'étude, les campagnols des champs (*Microtus pennsylvanicus*) ont été retirés de la région d'étude et les effets de ces retraits sur la population voisine de souris sylvestres ont été examinés. Le retrait d'une espèce est resté sans effet sur la répartition ou la démographie de l'autre espèce. Au cours de la seconde saison d'étude, les campagnols des champs ont subi une importante réduction de leur nombre et cette fluctuation naturelle a pu être utilisée comme expérience de retrait. Les populations de souris sylvestres n'ont pas été affectées, même si le déclin naturel de la densité des campagnols diminuait le nombre de campagnols dans la clairière de laîches plus efficacement que l'expérience précédente. Au cours de la troisième année, les campagnols des champs ont colonisé deux régions forestières où les souris sylvestres étaient les seuls habitants durant les deux saisons antérieures. Des campagnols à dos roux (*Clethrionomys rutilus*) ont aussi connu une recrudescence de leur population dans quatre territoires où leur nombre était très faible auparavant. Ni les campagnols des champs, ni les campagnols à dos roux n'ont affecté la répartition spatiale ou l'abondance des souris sylvestres. Il semble donc que les interactions compétitives n'aient pas d'influence sur l'utilisation du milieu ou sur l'abondance relative des espèces communes de petits mammifères dans le sud-ouest du Yukon.

[Traduit par le journal]

Introduction

Deer mice (*Peromyscus maniculatus*) are remarkably flexible in their habitat distribution, ranging from mature coniferous forests to grasslands. Red-backed voles (*Clethrionomys rutilus*) live in a variety of forest and shrubland habitats, frequently coexisting with deer mice. In contrast to the two previous species, meadow voles (*Microtus pennsylvanicus*) occur mainly in open habitats such as meadows, grasslands, abandoned fields, forest edges, and openings. These three genera dominate rodent communities in nonarid temperate habitats and often show contiguous populations between "forest species" and "grassland species."

What factors determine the use of habitats by these three species? Early observations on islands, where one species occupied a wider range of habitats in the absence of the others (ecological release), stimulated experimental work to test the hypothesis that competitive interactions between species were responsible for their habitat distribution (Grant 1972, 1978). However, the evidence accumulated on interactions between these three genera (*Peromyscus*, *Microtus*, and *Clethrionomys*) is contradictory (Grant 1972; Redfield *et al.* 1977; Abramsky *et al.* 1979; Hallet *et al.* 1983; but see M'Closkey 1975*a*, 1975*b*; M'Closkey and Fieldwick 1975; Morris 1983; King 1983; Martell 1983).

Alternatively, these temperate rodents have been described to be strong habitat selectors (M'Closkey 1975*a*, 1975*b*; M'Closkey and Fieldwick 1975; Morris 1983).

To test the hypothesis that competition is responsible for the differential habitat use (small overlap) and relative abundance among these three species, we used artificial and natural field experiments. In the first field season we artificially removed the meadow vole population from a sedge meadow adjacent to the forest where deer mice occurred alone. In the 2nd year a decrease in this cyclic population provided us with a natural removal experiment: voles were almost completely absent from the sedge meadow. The third summer, meadow voles colonized the forest, and red-backed voles, absent the previous 2 years, increased in numbers, providing natural introduction experiments.

The predictions for these situations from Grant's hypothesis are the following: (*i*) A change in resource use. In the absence of meadow voles in the contiguous habitat (removal experiment), deer mice will expand their use of habitats (niche shift or ecological release), showing a larger niche breadth and a larger niche overlap. In the presence of meadow voles and (or) red-backed voles in the same habitat (introduction experiments), deer mice will restrict their use of the habitat, showing a smaller niche breadth and smaller niche overlap. (*ii*) A change in numbers. Deer mice will increase in numbers after the removal of meadow voles (removal experiment). This might happen through higher immigration, lower emigration, higher survival and (or) higher reproduction. Deer mice will decrease in numbers after the introduction of meadow voles and (or) red-backed voles (introduction experiments).

Study area

The fieldwork took place at the south corner of Kluane Lake, Yukon Territory (61° N, 138° W), during the snow-free seasons (May to September) of 1981, 1982, and 1983.

The study was carried out in three different habitats: boreal forest, sedge meadow, and shrubland. The first two habitats have been described as vegetation zones by Hoefs *et al.* (1975). Shrubland includes successional stages of different ages.

The boreal forest, dominated by white spruce (*Picea glauca*), occupies the lower valleys from 770 to 1100 m. The density of different spruce stands and the presence of balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*) in some areas creates a variety of associations of dominant tree species that influence the shrub and herb undergrowth. These associations have been recognized as different plant communities (Douglas 1974) or habitats (Krebs and Wingate 1976). In this study we defined boreal forest as one habitat. The common species in the understory are soapberry (*Shepherdia canadensis*) in the shrub stratum and licorice root (*Hedysarum boreale*) and bearberry (*Arctostaphylos rubra*, *A. uva-ursi*) in the herb stratum.

The sedge meadow is mostly restricted to the margins of the lake. The fine-textured soils of this habitat are water saturated and in some areas flooding occurs during autumn because of the rising level of the underground water table (determined by rising lake level). A variety of sedges (*Carex* spp.), cottongrass (*Eriophorum angustifolium*), and other monocotyledons (*Juncus* spp.) are the most conspicuous plants in the meadow. Horsetails (*Equisetum palustre*) are very abundant, and small willow shrubs (up to 1 m) (*Salix glauca*) are widely scattered.

The shrubland habitat is less well defined and encompasses successional forest stages dominated by tall (1 to 3 m) willows (*Salix glauca*), balsam poplar, and white spruce in open stands. The shrubs are common in patches and along creeks close to the sedge meadows. Soapberry and licorice root are abundant in the understory.

Methods

Patterns

Since patterns of habitat use (habitat breadth, habitat overlap) and relative abundance change from year to year (Krebs and Wingate 1976), we determined habitat utilization patterns and abundance indices during the first field season (1981) by the use of snap-trap lines. Each line consisted of 20 stations with three "museum special" snap-traps per station (Krebs 1964; Krebs and Wingate 1976). Stations were spaced at 10-m intervals. The traps were baited with peanut butter, set for three consecutive nights, and checked daily. Throughout the summer we set 45 snap-trap lines in the following way: 13 in the forest, 14 in the sedge meadow, 10 in the ecotone between forest and meadow, and 8 in the shrubland habitat.

We used simple measures of niche breadth and niche overlap (Levins 1968; Colwell and Futuyma 1971; Southwood 1978, formulas 13.30 and 13.31, pp. 445 and 446).

We used both Cole's (C7) and Hulbert's (C8) coefficients of interspecific association to indicate the strength of the associations in the contingency table analysis (Cole 1949; Hurlbert 1969).

We used adjusted G log-likelihood tests (G_{adj}) to analyze the habitat distribution of captures at both snap-traps and live traps. Captures at live traps are not completely independent since the same individuals are sampled. To minimize this, we took into account only the first capture of every trap session.

TABLE 1. Experimental design. During 1981 and 1982 the grids occupied both meadow and forest habitats, and removal of meadow voles took place in the meadow habitat; during 1983 the grids were reduced to the forest habitat

Grid	1981	1982	1983
A	Control	Removal −meadow voles	
B	Removal −meadow voles	Control −meadow voles	Introduction +meadow voles
C		Control	Control
D			Control
E		Removal −meadow voles	Introduction +meadow voles +red-backed voles
G			Introduction +red-backed voles
H			Introduction +red-backed voles

Trapping technique

The experiments were carried out on livetrapping grids. We used Longworth live traps spaced at 10-m intervals. We prebaited the traps for 5 days and set them for two nights every other week or more often. Whole oats were used as bait and cotton batting as bedding. After every trap session the traps were locked open, allowing the animals to move in and out freely. Animals captured were ear-tagged with fingerling fish tags, and we recorded species, tag number, sex, breeding condition, body weight, and trap location. Breeding condition of males was assessed by recording their testes position as either abdominal (not breeding) or scrotal (breeding). For females we recorded vaginal status (open or closed), nipple size (small, medium, or large), condition of the pubic symphysis (closed, slightly open, or open), and evident pregnancies.

Experimental design 1981

During 1981 we used two livetrapping grids: an experimental (B.81) and a control (A.81). Each grid had 120 Longworth live traps arranged in a rectangular grid of 6 × 20 trap stations, covering an area of approximately 1.2 ha. Both grids were located in a similar way at the ecotone between spruce–poplar forest and sedge meadow. One-third of each grid (rows 14 to 20) was on the forest area while the other two-thirds (rows 1 to 13) were on the sedge meadow. The grids were parallel to each other and separated by 213 m (700 ft). Some of the snap-trap lines described above were near the livetrapping grids but never closer than 150 m (492 ft).

Beginning on the second trap session we removed all meadow voles caught at the experimental grid (B.81) every other week or more often. The aim of this manipulation was to reduce their population to observe the effects of such reduction on the contiguous population of deer mice.

Experimental design 1982

During 1982 we set four livetrapping grids. The two former grids were used in the same way as in the previous year, but the treatments were reversed. The control grid (A.81) in 1981 became the removal grid in 1982 and vice versa. We added a new grid (E.82) of similar size to the previous and situated also at the ecotone between the two habitats (Table 1).

This year, however, the population of meadow voles had become very scarce and stayed low throughout the summer. Therefore, the three grids are considered natural removal experiments. The only difference between the artificial removal treatment (A.82) and the

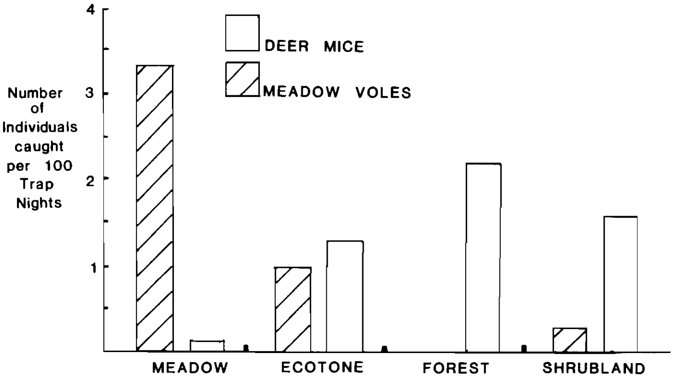

FIG. 1. Density indices for deer mice and meadow voles in different habitats for May to September 1981.

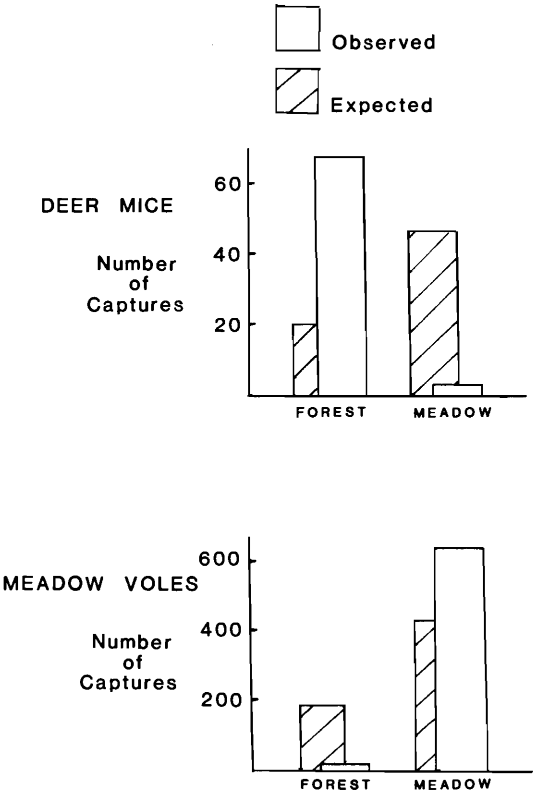

FIG. 2. Microhabitat use by deer mice and meadow voles on the control grid during 1981. Each species used one habitat and was rarely caught in the contiguous habitat.

other grids is that on the former we removed the few animals living there, reducing this population even further and keeping the habitat empty of *Microtus*.

The control grid (C.82) was located further away from the meadows in an advanced successional stage dominated by tall willows and a few spruce trees. It was a rectangular 4 × 10 grid occupying an area similar in size to the forest part of the removal grids. We trapped this grid from July to September.

Experimental design 1983

During the field season of 1983 we used six livetrapping grids. We reduced them to about one-third of their former size, leaving only the traps in the forest habitat. Their sizes ranged from 0.42 ha to 0.54 ha, and the number of traps ranged from 42 to 60. Two grids (B.83, E.83) were colonized by meadow voles. Three grids were colonized by red-backed voles (E.83, G.83, H.83). The other two grids (C.83, D.83) had very low numbers of red-backed voles and were considered controls. However, we made comparisons with grids in previous years also (Table 1).

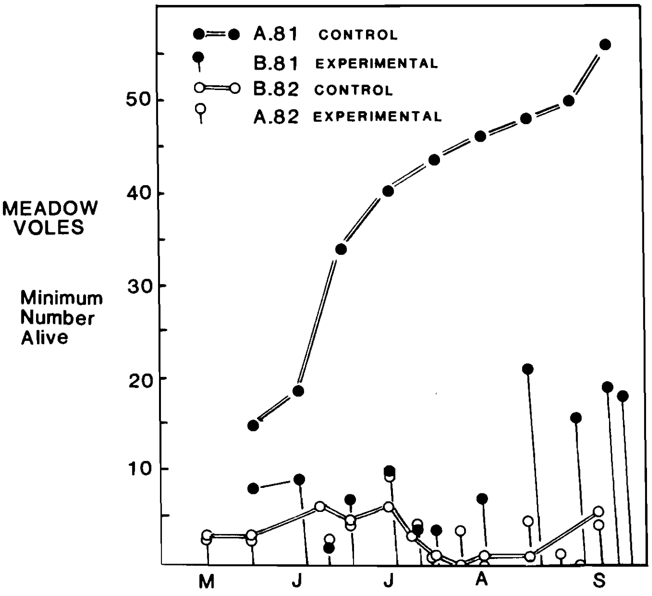

FIG. 3. Effect of the removal treatment on numbers of meadow voles. The natural decline during 1982 made the removal treatments more effective in reducing vole densities.

Results

Patterns of habitat use

Habitat use

The captures from snap-trapping lines (8040 trap-nights) indicated broad patterns of habitat use by both species during the summer of 1981. We caught nearly equal numbers of deer mice and meadow voles but in different habitats. Deer mice (n = 105) were caught mainly in the forest (47%) and secondarily in the shrubland (25%) and ecotone (24%) habitats. Very few (4%) were caught in the sedge meadow. In contrast, meadow voles (n = 108) were highly restricted to the sedge meadow (78%). Some were caught in the ecotone (18%) and fewer (4%) in the shrubland habitat, none was caught in the forest (Fig. 1).

A resource matrix analysis using these four habitats as different resource states indicates a larger habitat niche breadth for deer mice (B = 3.06) than for meadow voles (B = 1.76). Their habitat niche overlap is small (C = 0.313).

Microhabitat use

The habitat that showed the maximum overlap of both species was the ecotone. A closer analysis of the microdistribution in this area revealed prominent differences. To analyze this microdistribution we used the control livetrapping grid that was set perpendicular to the boundary between forest and meadow. Each habitat had a different proportion of live traps. The distribution of both species in these habitats was very different from that expected if the animals were using the habitats proportionally to the number of traps set in each. Deer mice were almost confined to the forest habitat ($G_{\text{adj}} = 130.71$, $p < 0.005$) while meadow voles were nearly confined to the meadow habitat ($G_{\text{adj}} = 465.31$, $p < 0.005$). Both species rarely used the shrubland habitat and were nearly absent from the habitat occupied by the other species (Fig. 2).

In summary, deer mice and meadow voles used distinct habitats and showed contiguous populations with small overlap

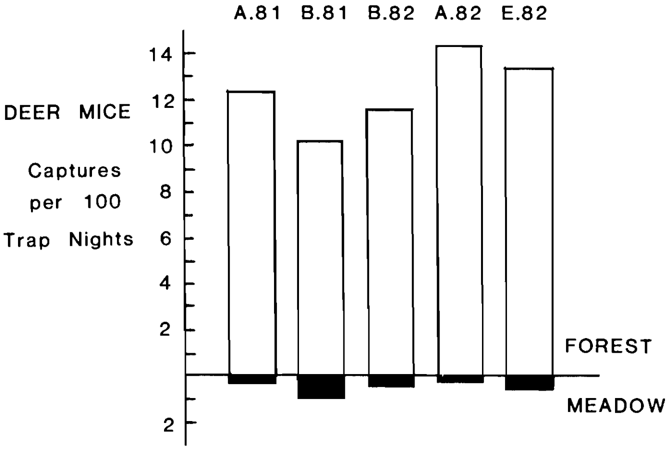

FIG. 4. Habitat use by deer mice. Deer mice were mainly confined to the forest habitat of the five livetrapping grids in spite of the absence of meadow voles.

when their habitats come into contact. Deer mice used a wider range of habitats. They were mainly found in the forest but used shrubland habitat too. Meadow voles, on the other hand, were mainly confined to the meadow habitat.

Removal experiments

We used four removal grids. During the first summer we used grid B.81 as an artificial removal grid. The natural decline of the meadow vole population during the second summer produced natural removal experiments in A.82, B.82, and E.82. Grid A.82 was subjected to an additional artificial removal to lower the population of meadow voles even further.

Effectiveness of removal manipulations

A major difficulty in using and interpreting the results of removal experiments is that animals living in surrounding areas continuously immigrate after the resident individuals have been removed. This immigration into the vacant area was strongly reduced during the second field season (1982) when the vole population decreased naturally. We used two ways to evaluate how effective the removal treatments (B.81, B.82, A.82) were at keeping the areas without voles. (*i*) By comparing the intensity of use (number of trap stations used per trapping session) in these treatments with that in the control. The mean number of trap stations used by *Microtus* per trapping session was 15 at B.81, 3 at B.82, and 2 at A.82. This translates into a reduction of use by *Microtus* of 53%, 91%, and 94%, respectively, in relation to the control grid in 1981, where 32 trap stations per trapping session were used on average. (*ii*) By comparing the intensity of use with the availability of trap stations in the meadow. The reduction is even more dramatic in relation to the number of traps available in the meadow. On the control grid, an average of 39% of the meadow traps were used by *Microtus* per trap session while only 22%, 4%, and 2% were used at B.81, B.82, and A.82, respectively.

A further indication of the effectiveness of the removal treatments is given by the number of individuals removed within trapping sessions. Voles were caught and subsequently removed either during the first or the second night of every trap session. In both grids (B.81, A.82) from which voles were artificially removed, most were removed on the first night and very few on the second. At B.81 the mean number of voles removed per trap session was 10.44, from which an average of 8.9 were removed on the first night, whereas only an average of 1.54 were removed on the second. At A.82, 3.44 individuals were removed every session on average. The average was 2.54 and 0.9 for the first and second night, respectively. This decline of animals removed within trapping sessions indicates that the area was almost free of voles after each session.

TABLE 2. Results of G log-likelihood test from comparisons of habitat use by deer mice in 1981 and 1982

Grid comparisons	Forest	Meadow
B.81 vs. A.81	1.08	5.50*
A.82 vs. A.81	0.54	0.54
B.82 vs. A.81	0.04	1.18
A.82 vs. B.82	1.20	0.22
B.82 vs. B.81	0.77	1.57
A.82 vs. B.81	0.08	1.18
E.82 vs. A.81	0.21	2.26
E.82 vs. A.82	0.18	0.96
E.82 vs. B.81	2.83	0.34
E.82 vs. B.82	0.68	0.30

NOTE: Expected values were obtained using trapping intensity (trap-nights). Only 1 out of 20 comparisons was significant. Habitat use by deer mice was similar in the grids regardless of the absence of meadow voles.

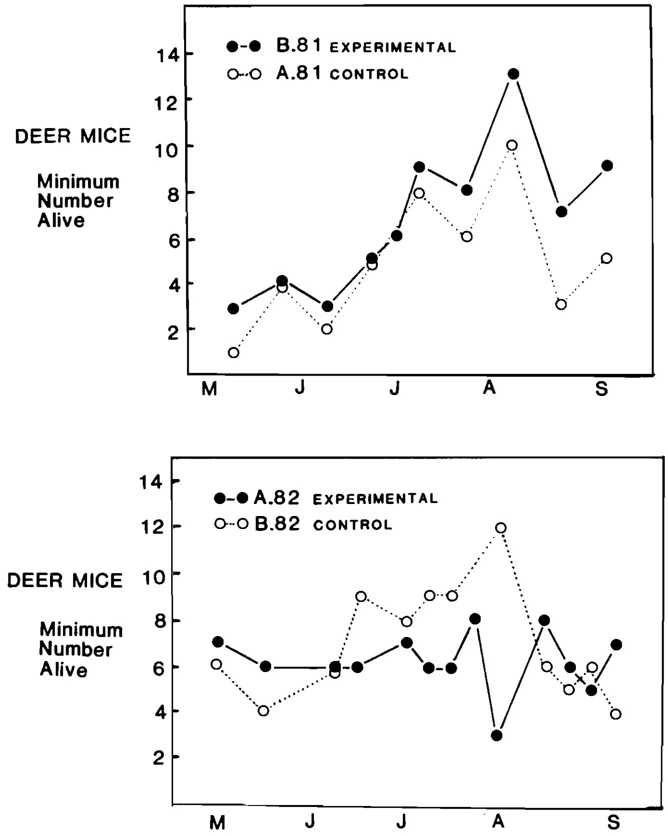

FIG. 5. Changes in minimum number alive of deer mice during 1981 and 1982 in both experimental and control grids.

In summary, the removal treatments were highly effective in reducing vole densities. This was more so during the second field season (1982), when the natural decline in vole numbers occurred. Figure 3 shows the effect of the removal treatments on numbers.

Spatial distribution

Did deer mice change their habitat use after the removal of meadow voles? Deer mice used mainly the forest habitat in the

TABLE 3. Deer mouse reproductive data, 1981 and 1982

	A.81 (control)	B.81 (artificial removal)	C.82 (control)	B.82 (natural removal)	E.82 (natural removal)	A.82 (natural + artificial removal)
Juveniles first trapped	Jul. 3	Jul. 3	Jul. 10	Jun. 29	Jul. 8	Jul. 8
End of male breeding season*	Jun. 18	Jul. 3	—	Jun. 17	Jul. 14	Jul. 14
End of female breeding season*	Aug. 1	Aug. 1	Jul. 29	Aug. 11	Jul. 14	Aug. 11
No. of litters (No. of females)†	2 (1)	2 (2)	1 (1)	5 (5)	6 (4)	5 (4)
No. of juveniles recruited‡	20	22	12	15	26	11
Juvenile productivity	10	11	12	3	4.3	2.2

*Last individual breeding.

†Adult females caught in two or more trapping sessions.

‡Juveniles tagged in the grid.

TABLE 4. Deer mouse survival data, 1981 and 1982 (minimum 2-week survival rates averaged over the spring and summer for adults and over the summer for juveniles, sexes pooled)

	A.81 (control)	B.81 (artificial removal)	C.82 (control)	B.82 (natural removal)	E.82 (natural removal)	A.82 (natural + artificial removal)
Adult survival						
Spring	0.66	0.92	—	0.76	0.7	0.9
	(4)	(4)		(8)	(6)	(10)
Summer	0.3	0.8	1.0	0.73	0.37	0.76
	(1)	(4)	(2)	(4)	(3)	(5)
Juvenile survival						
Summer	0.5	0.67	0.66	0.61	0.61	0.36
	(21)	(24)	(19)	(17)	(29)	(17)

NOTE: Sample size (number of individuals) is given in parentheses.

grids (A, B, E) both years (1981, 1982) regardless of the absence of meadow voles (Fig. 4). Only a small percentage of the total number of captures was recorded in the meadow habitat. From 20 comparisons (5 grids, 2 habitats), the only statistically significant difference appeared in their use of the meadow habitat at B.81 ($G_{\text{adj}} = 5.50$, $p < 0.025$) (Table 2). Several elements indicate that this difference was not related to the treatments. (*i*) The difference occurred in the grid where the removal of voles was least severe. Grids A.82 and B.82 had almost no voles present but there was no change in the habitat distribution of deer mice in these grids. (*ii*) The trap stations used in the meadow habitat at B.81 were located very close to the forest area. (*iii*) The same trap stations or others in the close vicinity were used during the second season (B.82) when there was no significant difference. (*iv*) Individuals that used meadow trap stations did not remain there. They were caught only once or twice and subsequently were recorded back in the forest. (*v*) Most of these individuals were juveniles probably attempting dispersal movements.

Population dynamics

Interspecific interactions may affect not only the spatial distribution (habitat use) of the species but also their local population density. Release from a negative interaction may result in higher reproductive rate, higher immigration, lower mortality rate or lower emigration, or a combination of these parameters. In fact, the populations of *Peromyscus* remarkably were similar in both 1981 and 1982 (Fig. 5).

Numbers

In general, populations of deer mice in the study area have a very low density in the spring, from 2 to 16 overwintered adults per hectare. Adult females have one or two litters. The first litter is born in mid-June and becomes trappable in late June or early July, whereas the second litter is born in mid-July and joins the trappable population in early August. The population increases through June and July and reaches its peak of 24 to 30 animals/ha in August. Little is known about the demography in winter, but there is never winter breeding.

During the 1st year, deer mouse populations on the control (A.81) and experimental (B.81) grids behaved very similarly. Both started with very low numbers in the spring and increased to a peak in August, then declined in the fall (Fig. 5). The population on the removal grid reached a slightly higher peak than that on the control and declined proportionally.

During the second field season the population of deer mice on B.82 behaved like that in the former year, increasing steadily through June and July to a peak in early August and declining subsequently. On the other hand, on A.82 numbers stayed very stable at an average of 14 per hectare throughout the summer (Fig. 5). In spite of the dramatic reduction of meadow voles in 1982, both populations of deer mice were slightly lower in 1982 than 1981.

Reproduction

The demographic machinery might be affected through changes in reproduction. Table 3 presents a comparison of the reproductive attributes between deer mice on experimental and control grids.

In early May when trapping began, all overwintered individuals had reached sexual maturity and were in breeding condition. Therefore we used the date when juveniles were first caught to compare the onset of breeding season on different grids. The populations bred synchronously, and juveniles were first caught during early July.

To estimate the end of the breeding season we recorded the last adult individual that showed signs of breeding condition. For males we recorded the testis in scrotal position and for females signs of lactation. The population sizes are too small to use 50% of the population breeding as a limit as other studies have done. Most adult males disappeared from the grids during mid-June to early July; thus the male breeding season was over. There was little overlap between adults males and juveniles. By the time juveniles became trappable, adult males had disappeared. The breeding season of females extended to late July and early August, when they stopped lactating.

By following the breeding condition of individual females, we estimated a minimum number of litters produced. Pregnancies were determined either by the size and shape of the females or by evidence of lactation. All adult females present had at least one litter and some had two.

Juvenile recruitment, the number of juveniles tagged for the first time on a grid, was very similar among grids in 1981. The second summer juvenile recruitment was lower even when more adult females were present and more litters were produced.

Juvenile productivity, the number of juveniles recruited per pregnant female, was similar on both grids during the first field season. In the second season, production of juveniles was low on the three experimental grids and high on the control. Considering both years, there seems to be a negative intraspecific relation between juvenile productivity and the number of breeding females (Table 3).

In summary, the grids were similar in their reproductive attributes. They were almost identical during the first summer. The second field season there was more variation but no consistent trend. Only juvenile productivity seems to show a consistent trend. It was low on the experimental grids. However, the fact that these three grids had the higher number of breeding females makes the result unclear.

Survival

Populations may be affected through changes in the rate of disappearance of individuals. Disappearance may be due either to mortality or emigration. In the following analysis these two sources are indistinguishable and are included in the survival rate.

Survival rate of adults was divided into two periods, spring (May and June) and summer (July, August, and September), when juveniles were also present. Juvenile survival was not divided into periods. Table 4 shows minimum 2-week survival rates averaged for adults and juveniles.

In 1981, survival rates were higher in the experimental grid, for adults both during spring and summer, and for juveniles. During 1982, spring adult survival was slightly higher than in the previous year. Summer adult survival was lower on the experimental grids than on the control, and juvenile survival was similar on all grids.

TABLE 5. Use of trap stations by pairs of species

Grid	Species	Fisher's exact test, p	Fager's index of affinity, z
B.83	*Peromyscus* vs. *Microtus*	0.53	0.617*
E.83	*Peromyscus* vs. *Microtus*	0.09	0.698*
E.83	*Peromyscus* vs. *Clethrionomys*	0.57	0.484
G.83	*Peromyscus* vs. *Clethrionomys*	0.18	0.632*
H.83	*Peromyscus* vs. *Clethrionomys*	0.87	0.852*

NOTE: In all cases, species use trap stations independently (Fisher's exact probability test). However, Fager's index of affinity shows that in four out of the five comparisons, trap stations are used by both species more often than by either alone. *, significant if larger than 0.5 (according to Fager 1957).

Introduction experiments

During 1983, two forest grids adjacent to the meadow habitat (B.83, E.83) were colonized by meadow voles, providing an introduction experiment with both year-to-year controls as well as contemporaneous controls. Similarly, red-backed voles increased from being nearly absent in the previous years. We compared the demographic parameters in four grids, two where red-backed voles and deer mice were about equally abundant (G.83, H.83) and two where red-backed voles were very scarce (no more than two individuals) (C.83, D.83).

Spatial distribution

Did the increase in numbers of meadow voles and (or) red-backed voles influence the distribution of deer mice? Neither meadow voles nor red-backed voles influenced the spatial distribution of deer mice. The distribution of these species was independent on all grids (Table 5). There were no negative associations as expected if interspecific interactions were influencing their distribution. Furthermore, Fager's index of affinity, which eliminates cell D (both species absent) from the contingency tables (Fager 1957), showed that voles and deer mice tended to use the same trap stations in four out of five grids. There were more trap stations used jointly than used by either species alone.

Population dynamics

Numbers

In two forest grids adjacent to the meadows (B.83, E.83) voles (*Microtus pennsylvanicus*) appeared during mid-May and early June 1983. They had been completely absent or in very low numbers in previous years. From very few individuals, they increased throughout the summer to a high peak in the fall, and became more abundant than deer mice. Deer mice, in turn, increased as in former years throughout the summer but did not decline in the fall. At the end of the trapping program deer mice were 1.5 to 3.5 times higher than in earlier years (Fig. 6). The colonization by meadow voles did not affect deer mice populations. This is further confirmed by comparing deer mice populations within the same year. The populations on grids where the colonization occurred (B.83, E.83) are very similar to those on the controls (C.83, D.83).

In a similar way, red-backed voles (*Clethrionomys rutilus*) colonized three grids (C.83, D.83, G.83), during early July 1983. At grid H.83, they were present from the beginning of the trapping program. The firsts two grids (C.83, D.83) never

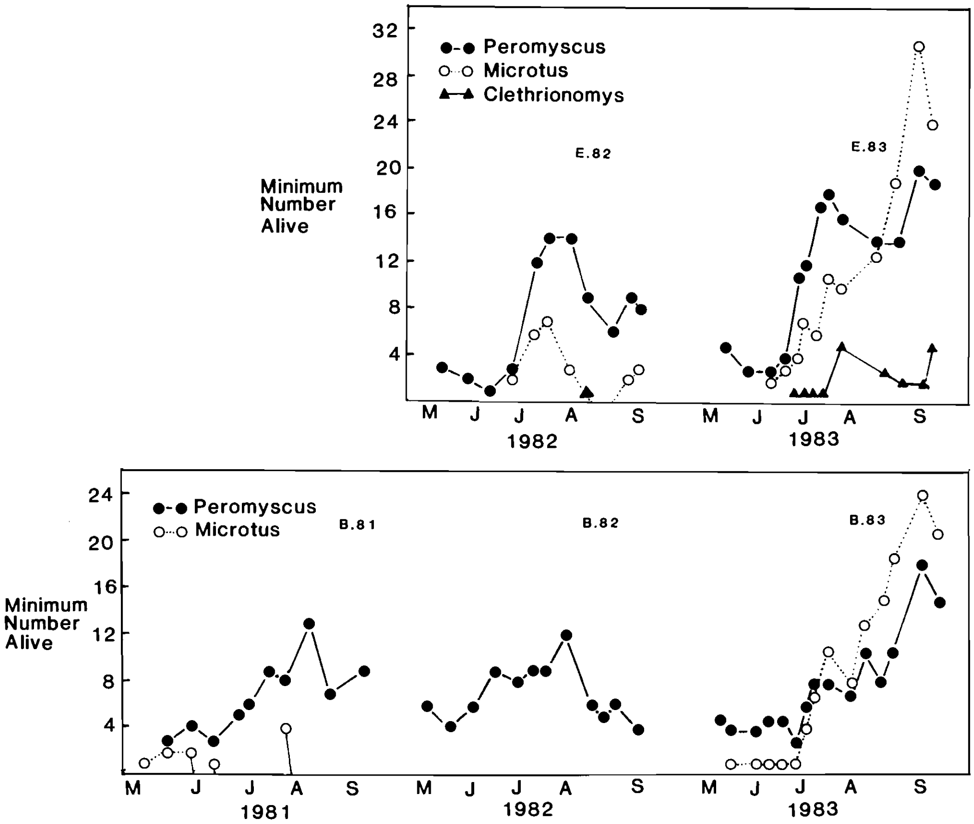

FIG. 6. Changes in minimum number alive of deer mice and meadow voles. The colonization of these two grids by meadow voles had no effect on deer mice numbers.

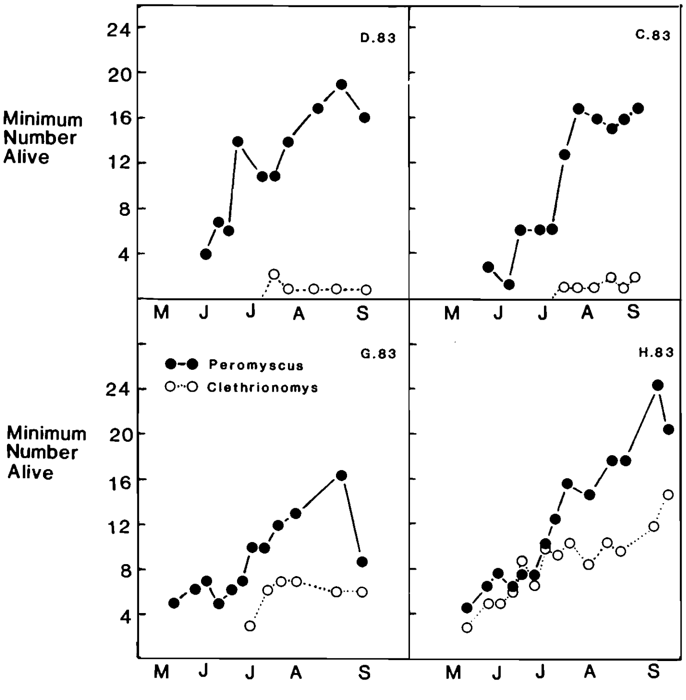

FIG. 7. Changes in minimum number alive of deer mice and red-backed voles in 1983. The populations of deer mice are very similar in the four grids regardless of the number of red-backed voles present.

supported more than two individuals. The third grid (G.83) maintained a medium to low density of 6 individuals (12/ha). The fourth grid (H.83) had a resident population of red-backed voles that grew parallel to the coexisting deer mouse population until July. Then it maintained an average of 11 individuals through the summer.

Deer mouse numbers on these four grids were much the same regardless of how many red-backed voles were present (Fig. 7).

Reproduction

If there is a negative interaction between these species, reproduction in deer mice might be affected by the presence of meadow voles and (or) red-backed voles in different ways. Deer mice might show a reduction in length of breeding season, number of breeding females, number of litters, litter size, or juvenile productivity. Table 6 compares the reproductive attributes measured between control and experimental grids.

The beginning of the breeding season was not documented, since both males and females were already breeding in early May when trapping started. The first juveniles were trapped from mid-June to late July. Two of the grids where red-backed voles were present had late recruitment of juveniles. Males ended breeding synchronously on most grids. Females, on the other hand, were more variable. The end of lactation ranged from mid-June to mid-August, with no consistent trend. The number of breeding females, number of litters, and juveniles recruited were higher where voles were present. Juvenile productivity, however, was more variable. The highest productivity was obtained at E.83, where both species of voles were present. This grid, however, was also being used for a deer mouse female removal experiment where adult females were removed after the first litter had been recruited.

Survival

The rate of disappearance of individuals might be affected directly, through behavioral interactions leading to emigration, or indirectly, through increased mortality. Table 7 shows minimum 2-week survival rates averaged for adults and juveniles.

Adult survival was divided into two periods: spring, when

TABLE 6. Deer mouse reproductive data, 1983

	Controls		Introductions			
	C.83	D.83	B.83, *M.p.*	E.83, *M.p.+C.r.*	G.83, *C.r.*	H.83, *C.r.*
Juveniles first trapped	Jun. 19	Jul. 2	Jun. 30	Jun. 23	Jul. 28	Jul. 9
End of male breeding season*	Jul. 19	Jul. 21	Jul. 19	Jun. 23	Jul. 19	Jul. 19
End of female breeding season*	Jun. 19	Aug. 15	Jun. 23	Jun. 23	Aug. 13	Jul. 9
No. of litters (No. of females)†	2 (1)	2 (1)	3 (2)	3 (2)	6 (3)	3 (2)
No. of juveniles recruited‡	13	18	23	34	22	18
Juvenile productivity	6.5	9.0	7.6	11.3	3.6	6.0

NOTE: *M.p.*, *Microtus pennsylvanicus*, *C.r.*, *Clethrionomys rutilus*.
*Last individual breeding.
†Adult females caught in one or more trapping sessions.
‡Juveniles tagged on the grid.

TABLE 7. Deer mouse survival data, 1983 (minimum 2-week survival rates averaged over the spring and summer for adults, and over the summer for juveniles, sexes are pooled)

	Controls		Introductions			
	C.83	D.83	B.83, *M.p.*	E.83, *M.p.+C.r.*	G.83, *C.r.*	H.83, *C.r.*
Adult survival						
Spring	0.66	0.79	0.54	0.82	0.74	0.94
	(9)	(9)	(9)	(7)	(8)	(10)
Summer	0.92	0.68	0.8	0.02*	0.81	0.91
	(1)	(7)	(1)	(6)	(5)	(8)
Juvenile survival						
Summer	0.91	0.74	0.84	0.79	0.63	0.76
	(29)	(27)	(29)	(38)	(24)	(24)

NOTE: *M.p.*, *Microtus pennsylvanicus*; *C.r.*, *Clethyrionomys rutilus*. Sample size (number of individuals) is given in parentheses.
*Low value due to an experimental adult female removal.

only overwintered adults were present, and summer, when juveniles had been recruited. Adult survival was very similar both during spring and summer in all the grids regardless of the presence of voles. Compared with that in previous years (Tables 4 and 7), spring adult survival was similar whereas summer adult survival was higher in the years when voles were present. Juvenile survival, in turn, was slightly lower at the grids where red-backed voles were present, but higher than in former years when deer mice were alone.

Discussion

Populations of deer mice were not affected by the removal of meadow voles from adjacent habitat. Neither the artificial removal of *Microtus* during 1981 nor their natural decline in numbers in 1982 influenced deer mouse spatial distribution or demography. Furthermore, neither the colonization of forest habitat by meadow voles nor the increase in numbers of red-backed voles during 1983 had negative consequences on the spatial distribution or population attributes of deer mice.

In contrast, populations of deer mice seem to perform better when another species is present. During 1982 when the decline of meadow voles occurred, deer mouse numbers were slightly lower. Conversely, in both forest grids colonized by meadow voles during 1983, deer mice reached higher numbers than in the previous year. Similarly, the grid that held the highest density of red-backed voles also supported the highest density of deer mice (Table 8). This suggests that these species might be affected by a common environmental factor.

TABLE 8. Summary of the effects of removal of meadow voles (*M.p.*) and introduction of meadow and red-backed voles (*C.r.*) on population parameters of deer mice

(A) Removals

	B.81 (artificial removal)	B.82 (natural removal)	A.82 (natural + artificial removal)	E.82 (natural removal)
Habitat use	+	0	0	0
Population density	0	0	0	0
Reproduction (juvenile productivity)	0	−	−	−
Survival				
Adult				
Spring	+	+	0	+
Summer	+	+	0	+
Juvenile (summer)	0	0	−	0

(B) Introductions

	B.83, *M.p.*	E.83, *M.p.+C.r.*	G.83, *C.r.*	H.83, *C.r.*
Habitat use	0	0	0	0
Population density	+	+	0	+
Reproduction (juvenile productivity)	0	+	−	0
Survival				
Adult				
Spring	−	+	0	+
Summer	0	*	0	0
Juvenile (summer)	0	0	−	0

NOTE: +, higher than control; 0, similar to control; −, lower than control.
*No adults present.

The results of this study are in agreement with the suggestion from observational studies that competitive interactions between *Peromyscus*, *Clethrionomys*, and *Microtus* have little influence in their habitat use and relative abundance (M'Closkey 1975*a*, 1975*b*; M'Closkey and Fieldwick 1975; Morris 1983; King 1983). On the other hand, the results contrast with early findings in enclosure experiments (Grant 1969, 1970, 1971, 1972; Morris 1969; Morris and Grant 1972) and removal experiments (Redfield *et al.* 1977; Abramsky *et al.* 1979).

Three possibilities may explain the disagreement between these results and other findings. First, competitive interactions among species of these three genera may be contingent on a number of different factors that change locally. Second, earlier studies may have interpreted their findings as competition when some other processes were responsible for the results. Third, competitive interactions may affect the populations of small mammals in our study area, but the manipulations and natural experiments were unable to detect them. We will discuss these three possibilities in turn.

First, interactions among species of these genera might be contingent on a number of local factors. The degree of similarity among resources utilized (food, habitat, nest sites), population densities in relation to resource availability, their species-specific aggressive behavior (level of tolerance and specificity) may all influence the relative importance of competition.

Are the species in this community utilizing similar resources? In relation to food resources, there is no strong basis to classify these genera as potential competitors, since their food habits are very distinct. Deer mice feed mainly on arthropods and seeds (Martell and Macaulay 1981); red-backed voles feed on lichens, fungi, and seeds (Martell 1981); and meadow voles feed on green parts of grasses and sedges (Banfield 1974). If we consider the possibility that their diet varies locally and that food overlap could be greater in the Kluane study area, then the colonization of forest habitat by meadow voles or the density increase by red-backed voles should affect the demography of deer mice, since populations of the last species in the area are limited by food supply (Gilbert and Krebs 1981). Nevertheless, as described above, *Peromyscus* populations were unaffected or else changed in the opposite direction to that predicted by the competition hypothesis.

Another potential resource that could be involved is nest sites. However, little is known about nest site requirements and specificity by these genera or the availability of this resource.

Most authors who claim that competitive interactions between these genera are important emphasize competition for space mediated through agonistic interactions (Grant 1972, 1978; Hawes 1976; Turner *et al.* 1975; Iverson and Turner 1972). In this study, however, both colonization of forest by *Microtus* and population increase by *Clethrionomys* took place during the breeding season, when the aggressive behavior of these species would have had the strongest effect. Nevertheless, the spatial distribution of deer mice did not change in the presence of coexisting species. Studies comparing island and mainland situations have documented differences in the frequency of aggressive behavior among populations of these three genera (Halpin 1981). If interspecific agonistic interactions are a proximate mechanism influencing the distribution of these genera, then such local variations in behavior would affect the intensity of interactions among them.

Douglass (1976) suggested that factors influencing habitat use and overlap between meadow voles and montane voles may change from place to place. In areas where the habitats of these voles are similar, behavioral interactions would be likely to operate, whereas in areas where the habitats are dissimilar, their distribution would reflect habitat preferences. If we incorporate the fact that some populations of voles show multiannual fluctuations, then influencing factors would change from time to time too. During years of low abundance, populations would be restricted to optimal habitats and at peak years a variety of habitats would be occupied, making interspecific interactions more likely to occur. The strong negative interaction between Townsend's voles and deer mice documented by Redfield *et al.* (1977) may be one extreme of this density gradient, since these voles sustain the highest average densities of any *Microtus* in North America (Taitt and Krebs 1985).

The second explanation for the inconsistency of findings is that other authors might have interpreted their results incorrectly. Earlier studies that provided support for the importance of competition, not only among these rodents but in community ecology in general (Grant 1969, 1970, 1971; Morris and Grant 1972), exhibit a number of drawbacks. They were carried out in enclosures that were small in relation to the rodents' home ranges. The movements of the individuals introduced were restricted. The areas were trapped out, and animals from elsewhere were introduced after spending some time in captivity. Once inside the enclosure they encountered a novel environment and foreign conspecifics. In one case, the species (red-backed vole) introduced was not found in the study site previous to its introduction. This may indicate that the habitat was not suitable in the first place. Since the responses documented are the result of the behavior of the animals, the conclusions may not represent the natural situation faithfully. Furthermore, one of the experiments had no contemporary control (Morris and Grant 1972) and none were replicated. In spite of all these drawbacks, the conclusions from these studies have never been questioned and are probably the most widely quoted evidence for competition among rodents.

In relation to removal experiments carried out in more natural situations, both studies that show a clear negative relationship between *Microtus* and *Peromyscus* (Redfield *et al.* 1977; Abramsky *et al.* 1979) underlined their uncertainty about the mechanism of the interaction.

The last possibility is that competitive interactions are important in the study area, but these experiments were unable to detect them. If the relative importance of competition changes with density, then the densities we found in the area during the last 3 years may not have been high enough to cause competition.

Deer mouse populations in the area change little from year to year and are limited by food (Gilbert and Krebs 1981); even when densities are low most available habitat is completely utilized because home ranges are large. There is enough intraspecific pressure for juveniles to leave the birth place and colonize the adjacent vacant habitat, but instead juveniles disperse long distances to other shrubby and forested habitats without making use of the closer meadow habitat. We think this is because these two habitats, forest and meadow, do not gradually merge into each other, but the ecotone is sharply discontinuous. Deer mice born in the forest would have a strong genetic preference for this habitat, reinforced by early experience (Wecker 1963).

In contrast, meadow voles and red-backed voles are much more variable in their numbers. This fact restricts the conclusions to the densities at which we found them. If they reach higher population numbers than those attained in this study, then competitive interactions may have a stronger influence. However, previous studies in the area have found densities similar to those recorded in this study (Krebs and Wingate 1976; Gilbert and Krebs 1981).

In spite of the number of studies on habitat use and competition among rodents, several areas remain obscure. Under which circumstances do interspecific interactions have an influence on populations of these small mammals? What is the magnitude of such influence in relation to the action of other factors? When interspecific competition does occur, what are the mechanisms of interaction? If we are to understand the dynamics of small mammal communities, the early generalization that competition for space among different species of rodents is a widespread phenomenon (Grant 1972, 1978) ought to be placed among a number of working hypotheses.

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