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COMPETITION BETWEEN *PEROMYSCUS MANICULATUS* AND *MICROTUS TOWNSENDII* IN GRASSLANDS OF COASTAL BRITISH COLUMBIA

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INTRODUCTION

Peromyscus maniculatus (Wagner) the deer mouse, can be divided into two subgroups: short-tailed, short-eared, and short-footed subspecies occupying grasslands, and long-tailed, long-eared and long-footed subspecies occupying woodlands (Baker 1968). *Peromyscus maniculatus austerus* (Baird), the subspecies found in coastal British Columbia in the Vancouver region is an enigma. It is a woodland species yet has short-feet and a relatively short tail (Cowan & Guiquet 1956; Sheppe 1961). Grant (1971) has suggested that the deer mouse suffers from competition from microtine rodents in grasslands, and is forced to live in the woods. Baker (1968) also notes that *Peromyscus* 'usually are secondary to *Microtus* in north temperate and boreal stands of perennial grasslands'.

Grant (1972) reviewed the experimental evidence for competition between *Microtus* sp. and *Peromyscus* sp. In his experiments little attention was paid to long-term changes in *Peromyscus* populations released from competition with *Microtus*. Grant was mainly interested in short-term changes in the rate of occurrence of *Peromyscus* in grass-land habitats following the removal of *Microtus*.

During our investigations into the population dynamics of *Microtus townsendii* (Bachman) and *M. oregoni* (Bachman) we have found several grassland areas with very low populations of *Peromyscus maniculatus*. These *Peromyscus* populations in grasslands could be low because of competition with *Microtus*. We have tested the competition hypothesis experimentally and report on the results here.

METHODS

General

We have systematically live-trapped the small mammals on twelve different grassland grids in three areas of the lower Fraser River Delta region of B.C. (Le Duc 1974; Krebs *et al.* 1976). Two of these areas have had large populations of *P. maniculatus*. The main study area is located on the abandoned Ladner Air Base about 10 miles (16 km) south of Vancouver, B.C. This grassland area is not cultivated and has been undisturbed for more than ten years. All of the grids we studied were open to movement to and from nearby areas.

Each of the grids covered an area of approximately 0·64 ha. All grids were trapped with 100 traps 7·6 m apart. Grids E and F were 5 × 20 stations arranged in a checkerboard. All other grids were 10 × 10. Each grid was trapped every other week. During the non-

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trapping period oats and cotton were made readily available in traps locked open. A heavy protective board was placed on top of the traps. During cool weather traps were set for two overnight periods and the intervening afternoon. In hot weather the afternoon trapping session was abandoned. No *Peromyscus* were killed in trapping.

At first capture, a mouse was tagged in the right ear with a numbered fingerling fish tag. At each capture the following information was recorded: number, grid location, sex, breeding condition (males: testes scrotal or not; females: vagina perforate or not, nipples small, medium or large, and pregnant or not). All mice were weighed to the nearest gram with spring scales and the presence of bot flies (Sadlier 1965) was recorded. Very few tagged *P. maniculatus* lost their tags.

Experiments

To test the hypothesis that deer mice are driven out of grasslands by *Microtus* species, we established two areas where all *Microtus* sp. were removed. One of these areas was located near the Serpentine River (Grid D of Krebs *et al.* 1976). Grid D and its control

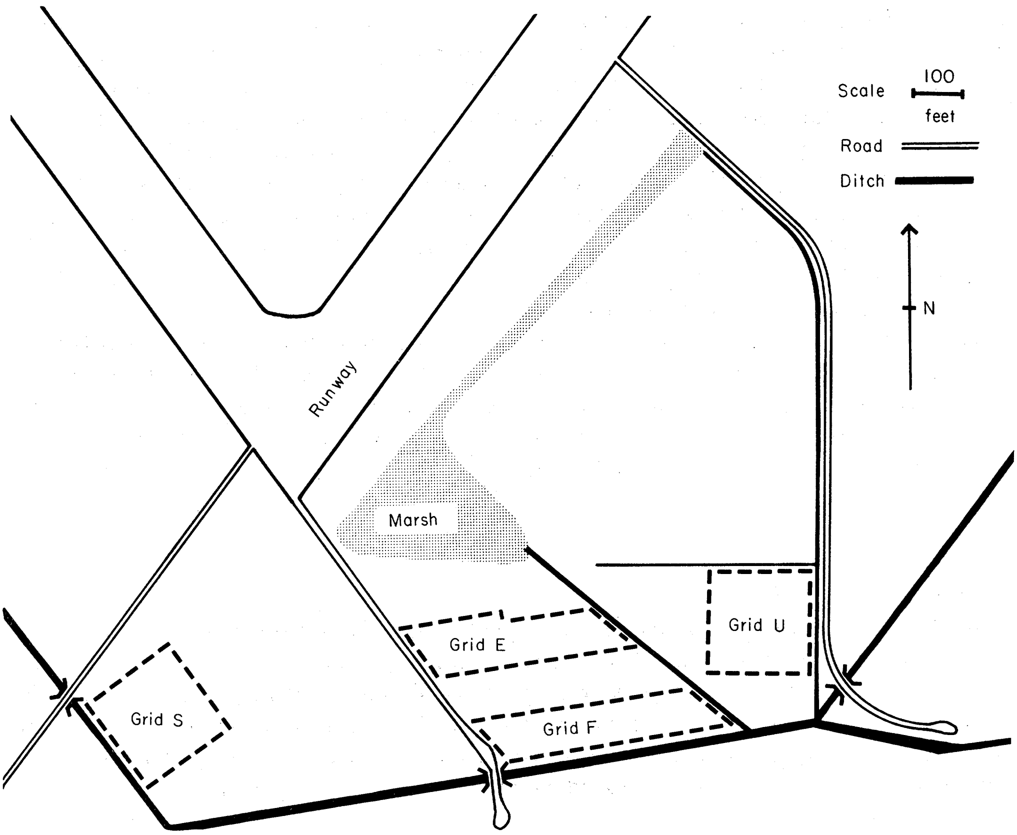

FIG. 1. Grassland study area at the Ladner Airbase, 16 km south of Vancouver, Canada. Grid E was a control area for all species; Grid F was an experimental grid from which all *Microtus* were removed; Grid U was an experimental grid from which most female *M. townsendii* were removed, and grid S was a similar area from which most male *M. townsendii* were removed.

grid (Grid C) had only a single species of *Microtus*, *M. townsendii*. Grid F and its control (Grid E) had two species of *Microtus*, *M. townsendii*, and *M. oregoni*. On the experimental grids, all *Microtus* were removed once every two weeks. In addition to the experimental Grid F and control grid E at Ladner Air Base, we had another grid, Grid U, which was used in experimental sex-ratio manipulation experiments on both species of *Microtus*. We followed the population changes in *P. maniculatus* on Grid U from July 1972 until July 1974. On all the other grids we followed population changes from July 1972 until September 1975.

Thus, we had a replicated experimental set up. Low number of *P. maniculatus* existed in all areas at the start of the experiment. We removed all *Microtus* from two of these areas and tested the hypothesis that *P. maniculatus* would increase in the absence of competition with *Microtus*. For the last 2½ months of the study we stopped removing the *Microtus* species from the experimental Grid F. We were interested to see if *Microtus* could actually drive out an established *Peromyscus* population. The locations of the areas and experimental design are given in Fig. 1.

RESULTS

Trappability

Rather than rely on estimates of population density, we have attempted to completely enumerate the populations on the areas we were studying (Hilborn, Redfield & Krebs 1976). Some deer mice weighed 8–11 g at first capture and were approximately four to six weeks of age. Other obviously older (pelage browner) deer mice were first caught at weights of 16–18 g. *P. maniculatus* is easily trapped. We estimated trappability by comparing the minimum number of animals known to be alive on a grid with the actual number caught. There was no difference in trappability of either sex. Trappability varied from 70 to 90% in most samples. Males on Grid U which contained *Microtus* were less trappable (71%) than males on the experimental grid where *Microtus* were removed (84%) ($\chi^2_{(1)} = 13{\cdot}04$, $P<0{\cdot}01$). This was not true for females ($\chi^2_{(1)} = 1{\cdot}28$, $P>0{\cdot}05$). Thus, one apparent effect of the presence of *Microtus* is to suppress slightly the trappability of male *Peromyscus*.

Population density

At the Serpentine River, *Peromyscus* responded dramatically to the removal of *Microtus townsendii*. As soon as we began removing *Microtus* on experimental Grid D *Peromyscus* colonized the area and maintained a viable population throughout the study. During the summer of 1973 the average density of *Peromyscus* on Grid D was thirteen individuals; during the summer of 1974 the average was six individuals. At the same time on the control Grid C, which had a dense, resident population of *M. townsendii*, not a single *Peromyscus* was caught during 1973 or 1974. These results are consistent with the hypothesis that *Microtus* excludes *Peromyscus* from grasslands.

At Ladner, *P. maniculatus* started at low density on the experimental Grid F, the control Grid E and Grid U. On the control Grid E, *Peromyscus* numbers remained low throughout the study at between zero and three; the *Microtus* density averaged close to sixty and then doubled over the last year of the study. On the Grid U, an increase started six weeks after trapping began and numbers went from one to ten in twelve weeks (Fig. 2). This increase slowed during late winter and early spring 1973, then burst again in late spring of 1973 with numbers reaching a peak of twenty-four in late summer 1973. Num-

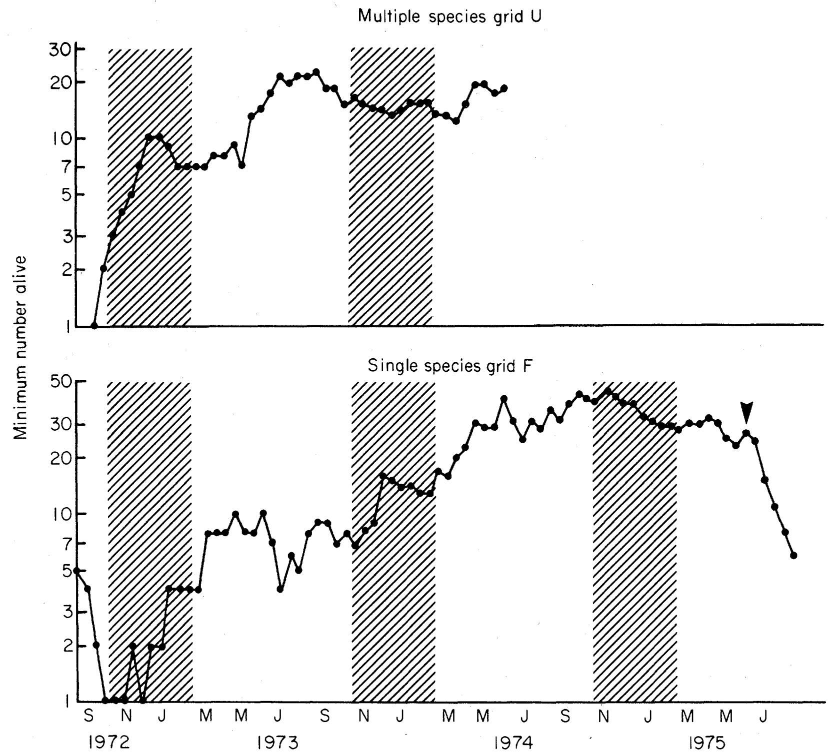

FIG. 2. *Peromyscus* population density on 0·64 ha plots; Grid U contained both *Microtus townsendii* and *M. oregoni* populations; all *Microtus* were removed from Grid F until 7 June 1975 (arrow) when *Microtus* were allowed to re-establish a resident population.

bers of *P. maniculatus* declined slowly on Grid U through the early winter of 1973 to 1974, then remained stable until the end of trapping on this grid in July 1974. The *Microtus* populations on Grid U were being constantly manipulated throughout this period. It had a very low density of female *Microtus townsendii* while the density of males ranged from twelve to fifty-five.

The number of *P. maniculatus* on the experimental Grid F started low (Fig. 2), declined to a single individual at the start of winter 1972, and then began a somewhat erratic increase to ten mice in spring 1973. Numbers fluctuated between four and ten until early winter 1973, when a rapid increase took the population to a winter peak of seventeen animals. The population declined slowly to a spring density of thirteen. With the onset of breeding in 1974, numbers increased to a summer peak in June of forty mice. After a slight decrease the population reached a winter peak of forty-four in November. Through the rest of winter 1974 numbers decreased slowly then remained fairly stable at between twenty-five and thirty-two into the summer.

From 18 June 1975, *Microtus townsendii* were allowed to recolonize the Grid F experimental area. In 10 weeks, the numbers of *P. maniculatus* declined from twenty-six to six, and the study was terminated. The number of resident *M. townsendii* went from zero to over seventy in the same period. Clearly, the recolonization by a resident population of *Microtus* on experimental Grid F caused a reduction in the number of *P. maniculatus*.

In summary, the number of *P. maniculatus* never reached more than three on the control grid E. In another population of *Microtus* sp. on Grid U the numbers of *P. maniculatus* were high and population trends resembled those in the experimental Grid F. *Peromyscus* densities were extremely low in all non-manipulated populations of *Microtus*. The single case of a multiple species grid where the *Peromyscus* population was able to establish a moderate density was Grid U, during the period from September 1972 to July 1974. The population of *Microtus* on this grid was being manipulated constantly in an effort to maintain a largely male population of *M. townsendii.* Since female *Microtus townsendii* appear to be more tightly regulated than males (Redfield, Taitt & Krebs 1977) it is interesting to speculate that females may also be more influential in intra-specific competition. In fact we have circumstantial data from a largely female *M. townsendii* grid (grid S, Fig. 1) that suggests that the density of *Peromyscus* there was low.

The *Peromyscus* population changes on the multiple species Grid U and the single species Grid F show some similarity. Both populations increased in number over the first winter, 1972. Grid U declined from ten to seven animals in the last half of this winter period. During the second nonbreeding season both populations again increased initially then declined slowly. The nonbreeding season on the single species Grid F was much shorter, the initial increase in number of mice was higher and the subsequent decline was less compared to the multiple species Grid U. This result supports the hypothesis of Petticrew & Sadlier (1974) namely 'that the length of the nonbreeding seasons governs the degree of decline in numbers which occurs during such seasons'. In this experiment the difference in the length of the non-breeding season is probably attributable to competition with *Microtus* on the multiple species grid.

Reproduction

P. maniculatus usually breeds in summer and goes out of breeding condition in winter (Sadlier 1974). We have not done a detailed autopsy program on dead mice. This is the best way to assess reproduction (Keller & Krebs 1970). We have, however, a rough index of the reproductive state of the population based on external examination of captured mice. We use both the percentage of adult (> 13 g) males with scrotal testes and the percentage of adult females with large nipples as our index.

In Table 1, we have presented the percentage of adult males with scrotal testes and the percentage of adult females with medium or large nipples on the multiple species Grid U and single species Grid F.

In all three years of the study males and females on Grid F started breeding during February. Males on Grid U were breeding in March 1973 and February in 1974. The onset of breeding in females on Grid U was during April 1973 and, apart from one female that was breeding in February 1974, females were breeding by March 1974. The percentage of both sexes in breeding condition during the summer months fluctuated on both grids. Breeding during summer 1973 reached a peak on both grids in July. The following year the intensity of breeding in both sexes on Grid F declined progressively during the last half of the season after the density of mice reached thirty in May 1974.

Males on both grids ceased breeding by October 1973. All females on Grid U stopped breeding in November 1973. On Grid F, January 1974 was the only month that no females were breeding that winter. The following winter, apart from two males that were scrotal in October the male nonbreeding season began in September 1974. Females on Grid F ceased breeding for December and January.

The reproductive activity of *P. maniculatus* was reduced in the presence of *Microtus* on on Grid U. The pattern of male reproduction was not appreciably changed. However,

Table 1. *Percentage of Breeding Activity in* Peromyscus maniculatus *per month; (sample size in parentheses)*

	Grid U		Grid F	
Period	Males	Females	Males	Females
1972				
Sept.	–	–	50 (2)	50 (2)
Oct.	–	–	100 (1)	–
Nov.	–	–	50 (2)	–
Dec.	–	–	0 (1)	–
1973				
Jan.	–	0 (2)	0 (1)	0 (1)
Feb.	–	0 (2)	50 (2)	50 (2)
March	100 (2)	0 (7)	67 (3)	100 (2)
April	100 (1)	57 (7)	80 (5)	33 (3)
May	50 (2)	50 (8)	33 (6)	57 (7)
June	67 (6)	71 (7)	63 (8)	40 (5)
July	100 (10)	75 (20)	100 (4)	67 (6)
Aug.	38 (8)	64 (14)	33 (3)	40 (5)
Sept.	20 (5)	13 (15)	50 (6)	100 (1)
Oct.	0 (10)	7 (16)	0 (3)	25 (4)
Nov.	0 (10)	0 (8)	0 (6)	50 (2)
Dec.	0 (4)	0 (10)	0 (9)	40 (5)
1974				
Jan.	0 (13)	0 (11)	0 (26)	0 (7)
Feb.	40 (10)	10 (10)	69 (13)	71 (7)
March	63 (8)	36 (11)	53 (17)	70 (10)
April	100 (9)	86 (8)	75 (12)	54 (13)
May	33 (6)	60 (10)	53 (17)	60 (15)
June	29 (7)	63 (8)	45 (20)	31 (16)
July	–	–	17 (18)	27 (33)
Aug.	–	–	8 (13)	62 (21)
Sept.	–	–	0 (14)	33 (18)
Oct.	–	–	8 (25)	11 (27)
Nov.	–	–	0 (19)	11 (19)
Dec.	–	–	0 (43)	0 (40)
1975				
Jan.	–	–	0 (8)	0 (8)
Feb.	–	–	32 (19)	25 (12)
March	–	–	72 (18)	43 (23)
April	–	–	52 (23)	48 (21)
May	–	–	31 (16)	87 (15)
June	–	–	67 (15)	67 (15)
July	–	–	77 (13)	36 (11)
Aug.	–	–	25 (4)	50 (6)

female *Peromyscus* in the presence of *Microtus* have a one to two month delay in the onset of breeding and their nonbreeding season was four months compared to one month for a non-competing population.

Survival

We have no effective method at present of sorting out the difference between emigration and death. What we can measure is the return of marked animals and this return we equate to survival. Survival is estimated as the minimum two-week survival as follows: the number of animals captured at time t, is divided into the number of those animals alive at time $t+14$ days. In Table 2 we give the minimum survival rate per fourteen-day period for both study plots.

Table 2. *Survival rates per* 14 *days in* Peromyscus maniculatus (*adults*≥13 *g; sample size in parentheses*)

		Grid U			Grid F	
Period	Males	Females	Total	Males	Females	Total
13 Sept.–18 Dec. 1972						
Adults	– (0)	– (0)	– (0)	0 (6)	0 (2)	0 (8)
Subadults	0·80 (5)	1·00 (7)	0·92 (12)	0·25 (4)	0·25 (4)	0·25 (8)
18 Dec.–25 March 1973						
Adults	1·00 (1)	0·88 (8)	0·89 (9)	0·80 (5)	1·00 (4)	0·89 (9)
Subadults	0·78 (9)	0·89 (19)	0·89 (28)	0·43 (7)	1·00 (2)	0·56 (9)
25 March–17 June						
Adults	0·86 (7)	0·89 (19)	0·88 (26)	0·76 (17)	0·85 (13)	0·80 (30)
Subadults	0·33 (3)	0·71 (7)	0·60 (10)	0·20 (5)	0·38 (8)	0·31 (13)
17 Jan.–23 Sept.						
Adults	0·74 (23)	0·94 (34)	0·88 (57)	0·67 (12)	0·80 (15)	0·74 (27)
Subadults	0·67 (18)	0·88 (16)	0·76 (34)	0·75 (4)	0·38 (8)	0·50 (12)
23 Sept.–19 Dec.						
Adults	0·88 (24)	0·89 (30)	0·89 (54)	0·82 (17)	0·89 (9)	0·85 (26)
Subadults	1·00 (4)	0·86 (14)	0·89 (18)	0·75 (4)	0·67 (3)	0·71 (7)
19 Dec.–27 March 1974						
Adults	0·90 (29)	0·97 (32)	0·93 (61)	0·91 (53)	1·00 (21)	0·93 (74)
Subadults	1·00 (4)	1·00 (2)	1·00 (6)	0·78 (9)	0·25 (4)	0·62 (13)
27 March–19 June						
Adults	0·76 (21)	0·79 (29)	0·78 (50)	0·81 (43)	0·86 (44)	0·84 (87)
Subadults	0·55 (11)	0·82 (17)	0·71 (28)	0·90 (10)	0·83 (18)	0·86 (28)
19 June–25 Sept.						
Adults				0·72 (50)	0·80 (66)	0·77 (116)
Subadults				0·65 (23)	0·71 (34)	0·68 (57)
25 Sept.–18 Dec.						
Adults				0·86 (77)	0·94 (82)	0·90 (159)
Subadults				0·86 (21)	0·87 (23)	0·86 (44)
18 Dec.–26 March 1975						
Adults				0·79 (63)	0·93 (60)	0·86 (123)
Subadults				1·00 (7)	0·78 (9)	0·86 (16)
26 March–20 June						
Adults				0·70 (54)	0·69 (55)	0·70 (109)
Subadults				1·00 (11)	0·30 (10)	0·67 (21)
20 June–27 Aug.						
Adults				0·67 (39)	0·67 (36)	0·67 (75)
Subadults				0·54 (13)	0·43 (14)	0·48 (27)

Survival rates were high on Grid U. Total adult survival only fell below 0·88 in the last period of the study. Adult females survival was particularly high ranging from between 0·88 and 1·00 in all but the last period. Adult male survival tends to fall off with the onset of breeding reaching its lowest point during the last half of the breeding season in 1973. Sub-adult survival is lowest early in the breeding season and increases progressively to a maximum over the winter.

Survival on experimental Grid F was poorer than on Grid U. For the first five months on the single species grid, survival was very poor, averaging 10% per fourteen days. Survival increased at the end of the first non-breeding season, and remained high until the second half of summer 1973. Survival rates increased during autumn 1973 and winter 1974 and declined at the onset of breeding in 1974.

The patterns of survival in each age and sex group are similar to those on Grid U. Adult females have generally the highest survival, although like the adult males their survival declines after the onset of breeding in 1975 the year with the highest breeding density. Survival of all groups declined dramatically during the last period as *Microtus* became resident on the grid. Generally survival rates were highest in the nonbreeding season on both study areas.

We have attempted to index early juvenile survival using a method modified from Krebs (1966);

$$\text{Index}_t = \frac{\text{No. mice less than 10 g in week } t}{\text{No. females with medium to large nipples in time } t-2 \text{ weeks}}$$

This method runs into some problems when there are few animals and the denominator is zero. Thus, we have summed over periods. The index of early juvenile survival on Grid U was poor throughout the duration of the study, especially when compared to experimental Grid F. Although there were large numbers of females lactating on Grid U, very few young were captured. The index of early juvenile survival on experimental Grid F was higher than on Grid U but was bad during the period 11 February to 26 August 1974, a period of peak numbers. The index of early juvenile survival was 0·29 (i.e. there were 0·29 young captured for every lactating female) on Grid U, and 0·51 on the experimental Grid F. Thus, the removal of *Microtus* from experimental Grid F increased early juvenile survival.

DISCUSSION

The results of our experiments clearly demonstrate that *P. maniculatus* can establish grassland populations in coastal British Columbia and that these populations can reach high densities. It is also clear that *Microtus* sp. are a sufficient cause responsible for the lack of *P. maniculatus* in the grasslands we studied.

If we compare the experimental grids with the control grids both at Ladner Air Base and at Serpentine River, we conclude that *Microtus* was actively excluding *P. maniculatus* from grassland area. When we removed *Microtus, P. maniculatus* increased to a remarkably high density and stayed at this high level until *Microtus* were allowed to recolonize the area; then *P. maniculatus* declined rapidly.

But a high density of Peromyscus was also found on Grid U which contained two species of *Microtus*. This observation needs to be reconciled with the competition hypothesis. Grid U was not strictly speaking a control grid since we were involved in experimental manipulations of the sex-ratio of the two *Microtus* species (Redfield *et al.* 1977). These manipulations may have altered social organization significantly in the *Microtus* populations. The density of female *M. townsendii* was kept low on Grid U. If female *Microtus* are the principal agents of interspecific interference, the establishment of *Peromyscus* on Grid U could be explained.

What is the mechanism by which *Microtus* excluded *P. maniculatus*? Survival of resident *P. maniculatus* in the presence of *Microtus* was reduced during the recolonization of Grid F. Thus, *Microtus* reduces the survival or increases the dispersal of resident *P. maniculatus* of all size classes.

On June 6 1975, we stopped removing recruiting *Microtus* and we compared the recruitment of new *Peromyscus*. From April 7 to August 27 1975 we caught thirty-seven new mice. Thirty-three of these were first caught prior to the establishment of a resident population of *Microtus*. Only four *P. maniculatus* were first caught after *Microtus* were allowed to colonize the area. In the previous year of 1974, of the seventy-four new captures from April 8 to August 28, forty-two were caught in the first twelve weeks and thirty-two in the last ten weeks. Clearly, *Microtus* also prevents the recruitment of *P.*

maniculatus and this effect coupled with the increased loss rate prevents the build-up of *Peromyscus* populations.

We now turn our attention from the competitive aspects of this study to a few general considerations of the population dynamics of deer mice in a grassland area. All previous work on deer mice in coastal British Columbia has been on populations in forested regions (Sadlier 1974). In forested areas a density of thirty mice per ha at the end of the breeding season was typical (Petticrew & Sadlier 1974). The general pattern of population change of forest *Peromyscus* (Sadlier 1965) is for populations to reach peak densities in autumn.

Our populations reached maximum densities of thirty-four mice per ha (Grid U) and sixty-one mice per ha (experimental Grid F). Not only were these densities very high, but the changes in population density throughout the year were somewhat different from populations in the forest. Our grassland populations reached peak numbers in the middle of the breeding season as well as during the winter. The behavioural mechanisms outlined by Sadlier (1965) for regulation of numbers in forest *Peromyscus* may be somewhat different in grassland deer mice.

Our experimental work supports the conclusion of Grant (1971) that *Peromyscus* suffers from competition from *Microtus* in grasslands. The puzzle we do not understand is why this competition should exist at all. Some resource ought to be in short supply for competition to occur. The food resources of *Peromyscus* and *Microtus* are very different and competition for food seems unlikely (but possible). Resources associated with space —burrow sites—seem even less likely to be in short supply. Thus we have a dilemma of clear evidence of competition between these two genera of rodents but no explanation of why in an evolutionary sense *Microtus* should bother to exclude *Peromyscus* from grasslands.

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SUMMARY

(1) *Microtus* sp. were removed from two grassland areas south of Vancouver, British Columbia, over three years in order to test the hypothesis that *Microtus* sp. competitively exclude *Peromyscus maniculatus* from grasslands. Social organization of *Microtus* on a third area was disrupted for two years and the demographic fate of *P. maniculatus* on these manipulated areas was compared.

(2) *Peromyscus* populations increased dramatically to sixty-one mice/ha within two years of the continuous removal of *Microtus* from one grassland area. *Peromyscus* populations also increased dramatically to thirty-four mice/ha in an area where the social organization of the resident *Microtus townsendii* was disrupted by manipulation of the sex-ratio of *Microtus* toward a shortage of females. Virtually no *Peromyscus* lives on the control area which had a normal *Microtus* population.

(3) In the absence of *Microtus* the trappability of male *Peromyscus* was 9% higher than in the presence of *Microtus*.

(4) Survival of *Peromyscus* was remarkably high on all study areas, especially in winter and spring. There were no indications of a decline in survival rates with the onset of breeding.

(5) Reproduction of *Peromyscus* appeared to start earlier in the year and last later in autumn in the absence of *Microtus*.

(6) When *Microtus* were allowed to recolonize an experimental grid, the number of *Peromyscus* dropped dramatically within six weeks. The cause of the decline in the number of *Peromyscus* was traced to an almost complete exclusion by *Microtus* of newly recruiting *Peromyscus* and an increase in mortality or dispersal in adult *Peromyscus*.

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