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POPULATION REGULATION IN DEER MICE: THE ROLE OF FEMALES

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SUMMARY

(1) The influence of adult females on juvenile survival was assessed in a northern population of deer mice *Peromyscus maniculatus* during the snow-free season of 1983.

(2) Removal of breeding females from two areas resulted in a higher recruitment of juveniles. This was due to an increase in the survival of resident juveniles during their first month of life before they were recruited into the trapable population.

(3) Survival of all trapable juveniles did not differ between experimental and control areas.

(4) Production (number of juveniles recruited per female) was negatively related to the number of breeding females and unrelated to the number of breeding males.

(5) Densities were 1·5–3 times higher in the female removal grids than in the control grids during late July.

(6) Migration of adults during the breeding season was strongly biased towards males. There was no apparent sex bias in migration among juveniles.

(7) Thus, in the study area in the southern Yukon female deer mice determine juvenile recruitment, and males are unimportant in population regulation.

INTRODUCTION

Populations of deer mice (*Peromyscus maniculatus* (Wagner), *P. leucopus* (Rafinesque), *P. polionotus* (Wagner)) show annual fluctuations and reach similar densities year after year (Sadleir 1965; Terman 1968; Fairbairn 1977; Sullivan 1977; Gilbert & Krebs 1981; Taitt 1981; Millar 1982). Densities are low in spring and increase with the recruitment of juveniles during late summer and autumn. Peak densities occur during autumn and winter (October–November) and then decline to low numbers in spring. This pattern varies somewhat with habitat (Millar 1982), latitude (Mihok 1979; Gilbert & Krebs 1981; Millar 1982) and on islands (Sullivan 1977). Irruptions have been documented, but they seem to be exceptions (Sullivan & Krebs 1981; Sexton *et al.* 1982).

Most authors agree that social interactions among members of the population play a major part in affecting the annual fluctuation in numbers (Sadleir 1965; Healey 1967; Metzgar 1971; Petticrew & Sadleir 1974; Fairbairn 1977; Taitt 1981). Spacing behaviour of dominant individuals is thought to influence the emigration or mortality of subordinate members. However, there is ambiguous evidence about both the extent that each sex influences population dynamics and the nature of the interactions.

Some studies have provided support for the hypothesis that adult males affect the survival of juveniles during the breeding season (Sadleir 1965; Healey 1967; Petticrew & Sadleir 1974; Fairbairn 1977). There is also indirect evidence from laboratory

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environments (Savidge 1974a,b; Rowley & Christian 1976; Ayer & Whitsett 1980; Gleason, Michael & Christian 1980; Wolff 1985) and from natural populations (Fordham 1971; Metzgar 1971, 1979; Hansen & Batzli 1978; Taitt 1981) which indicates that females could have an important effect on the population dynamics.

Populations of deer mice in the Yukon differ from those at lower latitudes. They live at lower densities and have shorter breeding seasons; only one or two litters are produced. The first litter averages 6·0 young (S.D. = 0·63, $n = 11$) and the second averages 5·1 young (S.D. = 1·7, $n = 7$). In addition, juveniles do not reach sexual maturity during their first year of life.

In this study, we investigated the effect of breeding females on the dynamics of populations of deer mice in the Yukon. We hypothesize that breeding females exert a negative influence on the juvenile population. The prediction from this hypothesis is that in the absence of breeding females, juveniles will show increased survival.

STUDY AREA

The field work was carried out in the boreal forest at the south corner of Kluane Lake, Yukon Territory (61°N, 138°W) from May to September 1983. The forest is dominated by white spruce (*Picea glauca* (Maench) Voss). In some places there are mixed associations with balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx). The understorey is dominated by soapberry (*Shepherdia canadensis* (L.) Nutt.), willow shrubs (*Salix spp.*) and small herbs such as liquorice root (*Hedysarum boreale* Nutt.), and bearberry (*Arctostaphylos rubra* (Rehd., Wils) Fern. and *A. uva-ursi* (L.) Spreng).

METHODS

Seven small grids (A, B, C, D, E, G and H), 200–2000 m apart were live-trapped. Grids A, B, C and E were trapped during 1982 and A and B also during 1981. Data from 1981 and 1982 were included only in the analysis of production. Grids varied in size from 0·42 to 0·60 ha and in the number of traps from forty-two to sixty. Longworth traps were spaced at 10-m intervals, and provided with cotton as bedding material and oats as bait. Traps were prebaited for 2 days before the first trapping session. Trapping sessions lasted 2 nights and took place every 10 days or more often. Traps were locked open and left on site between trap sessions. All individuals caught were ear-tagged and their location, sex, weight and breeding condition were recorded. Grids B, C, D, G and H were used as controls where no manipulation was undertaken. Our definition of juveniles includes all young of the year, even if they had attained adult size (>20 g). Most grids were used by red-backed voles (*Clethrionomys rutilus* Pallas) or meadow voles (*Microtus pennsylvanicus* (Ord)). Interspecific interactions between these two species and deer mice have been discussed elsewhere (Gilbert & Krebs 1984; Galindo & Krebs 1985).

Female removals

Grids A and E were used for female manipulation experiments. Adult females were removed from these areas immediately after the juveniles from the first litter began entering live traps. After the removal of resident females, all new adult females moving onto the grid were subsequently removed.

On grid A all resident females removed were caged in the centre of their home ranges.

Cages were rectangular (80 × 25 × 25 cm) and made of plywood with wire mesh at both ends. The size of the mesh (12 mm) was selected so that only juveniles could move in and out. In this way a second litter could be produced in contrast to grid E where resident females were totally removed. Inside the cages on grid A, adult females were constrained and prevented from interacting with other individuals in the population. Cages were provided with nesting material, sunflower seeds, oats, and water *ad libitum.*

Total removals

Two total removal grids (X, Z) were used to measure the migration of individuals into empty habitats. Each grid had forty-nine stations and two Museum Special snap-traps per station. Stations were spaced every 10 m and each grid covered 0·49 ha. The grids were approximately 400 m apart and separated by the Alaska Highway. Traps were baited with peanut butter and were set every 10 days for three nights; between sessions they were set off and left in place. We recorded sex, weight, breeding condition and trap location of all individuals caught, and each mouse was autopsied to analyse reproductive attributes in detail.

RESULTS

Female removals

On grid A there were two resident females with mutually exclusive home ranges (Fig. 1). They were caged in approximately the centre of their home ranges on 20 June 1983. They gave birth to second litters around 28 June 1983. These juveniles became trapable 3 weeks later (19 July 1983). After the confinement of these two females no other breeding females were caught on this grid. Two of the three males living on this grid disappeared after the females were confined.

In grid E there were also two resident females and their home ranges overlapped a little (Fig. 1). They were removed on 24 June 1983. After the removal, the three resident males disappeared. Through July, four more immigrant breeding females were caught and removed.

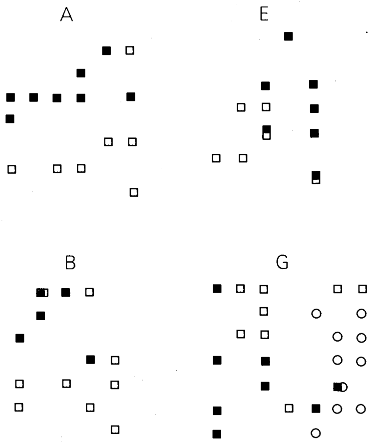

FIG. 1. Spatial distribution of the breeding females of *Peromyscus maniculatus* on four grids (A, E, B, G) during May and June 1983. Each figure illustrates individual females and their trap locations (different symbols for each female). Females had non-overlapping home ranges. Traps were 10 m apart.

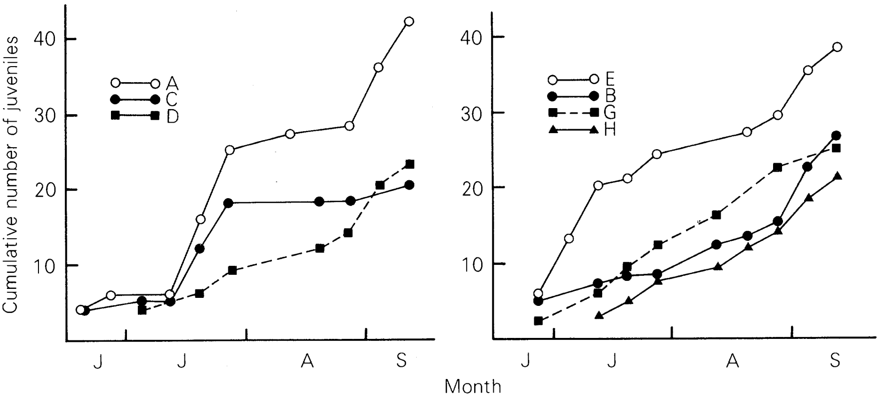

FIG 2. Cumulative number of juveniles recruited in experimental (A, E) and control grids (C, D, B, G, H) in 1983.

Recruitment

The removal of females affected juvenile recruitment. The total number of juvenile recruits was 1·5–2 times higher on both experimental grids than on the controls (Fig. 2). The data were subdivided into two periods of recruitment. The first period includes late June and July, and the second August and early September. These periods coincide approximately with breeding and post-breeding seasons. During the first period there were more juveniles recruited in the female removal grids than in the controls (*t*-test, d.f. 5, $P < 0{\cdot}005$). During the second period there was no significant difference in recruitment between experimental and control grids (*t*-test, d.f. 5, $P > 0{\cdot}2$). Therefore, the main response to the experimental removals occurred during June and July. However, there were some differences between experimental grids in the timing of the response.

On grid A, juvenile recruitment increased during late July. There was little change through August and a second pulse of recruitment occurred during early September. However, this late pulse also occurred at some control grids. A total of forty-two juveniles were recruited. On grid E, juvenile recruitment increased shortly after the removal of breeding females. In this grid the main response took place during early July. A total of thirty-eight juveniles were recruited (Fig. 2).

Four control grids (B, D, G, H) produced similar patterns of results (Fig. 2). They all had low, but constant recruitment throughout the summer. The fifth control grid (C), showed some resemblance to the experimental grids in that recruitment was moderate during July. After this, no juveniles were recruited during August and very few in early September. This control grid had the lowest number of breeding females ($n = 1$).

The sex ratio of juveniles caught on the controls was even. Similarly, the female removal grids had even sex ratios among recruited juveniles (Gadj. log-likelihood tests, all $Ps > 0{\cdot}05$). This was true for both the total number of juveniles caught during the entire season and for juveniles caught during the breeding season (late June and July).

Further analysis indicates that the increase in recruitment in the breeding season was due to resident juveniles rather than to immigrants. On the total removal grids juveniles that arrived during July weighed an average of 18 g (Fig. 3). Thus, two categories were defined: juveniles first trapped when they were 15 g or less were considered *residents*. The rest (16 g or more) could either be immigrants or resident juveniles. Given this definition, the number

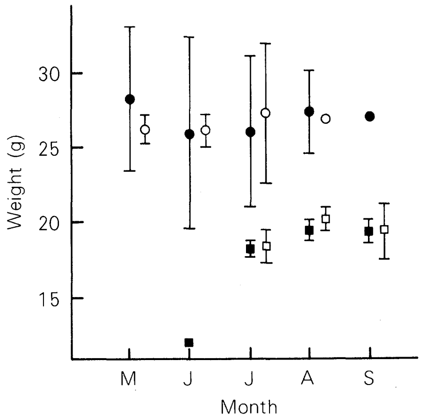

FIG. 3. Average weight and 95% confidence intervals for deer mice trapped on the total removal grids: (●) adult males; (○) adult females; (■) juvenile males; (□) juvenile females. Both grids combined.

of resident juveniles recruited during June and July was significantly higher in the female removal grids than on the control grids (t-test, d.f. 5, $P < 0{\cdot}01$). On the other hand, the number of juveniles recruited from the second category was not significantly different between experimental and control grids (t-test, d.f. 5, $P > 0{\cdot}1$). Therefore, most of the effect can be attributed to an increase in the number of resident juveniles recruited.

On grid A, from seventeen resident juveniles recruited during June and July, 35% belonged to the first litter, whereas 65% were second litter juveniles (born in cages). On grid E, all the fourteen resident juveniles recruited during these 2 months belonged to the first litter. This difference in recruitment of first and second litters among female removal grids explains the differences noted in the timing of the response.

Survival

As in other studies, our measure of survival includes both death and emigration. Juvenile survival was analysed within the same two periods as in the analysis of recruitment.

When all juveniles were considered, survival rates in the trappable population did not differ between experimental and control grids. This was true for the period of June–July as well as for August–September (t-tests, d.f. 5, $P > 0{\cdot}2$).

Similarly, the comparison of first litter survival between experimental and control grids showed no significant differences. Average 2-week survival of first litter juveniles was similar for both periods: June–July and August–September (t-tests, d.f. 5, $P > 0{\cdot}4$).

Production

An index of production was calculated for every grid using data for 1981, 1982 and 1983. This index is the number of juveniles recruited divided by the average number of breeding females. The experimental grids were excluded from this analysis since it is not possible to obtain the index when no females are present. This index of production was inversely related to the number of breeding females ($\log y = -0{\cdot}24x + 1{\cdot}55$, $n = 11$, $P < 0{\cdot}001$) but unrelated to the number of breeding males ($\log y = 0{\cdot}01x + 1{\cdot}06$, $n = 11$, $P = 0{\cdot}75$) (Fig. 4). A similar relationship was found for data from the control grids of Gilbert & Krebs (1981). They worked in the same area from 1976 to 1979 with grids

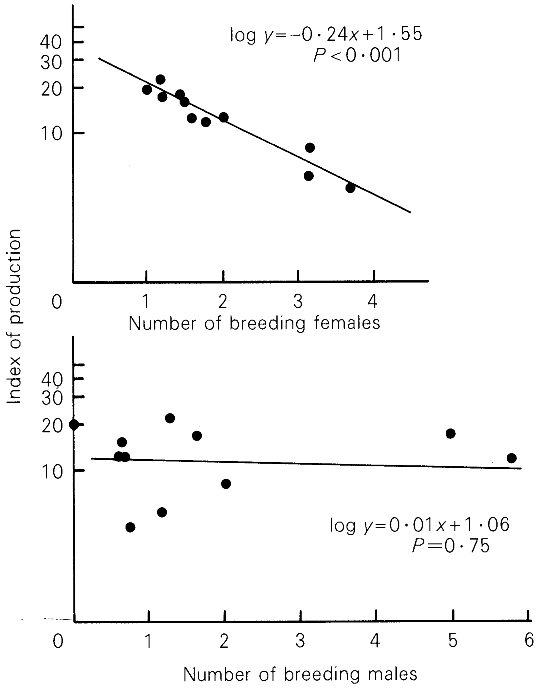

FIG. 4. Index of production (number of juveniles recruited per breeding female) in relation to the average number of breeding females and males. Each point represents one grid during one field season. Data from 1981, 1982, and 1983 are included.

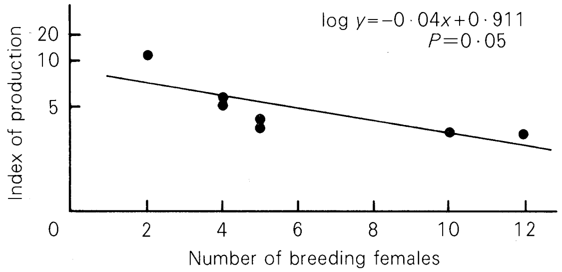

FIG. 5. Relationship between the index of production and the number of breeding female deer mice from the data of Gilbert & Krebs (1981).

approximately four times larger. Their data show an inverse relationship between the index of production and the number of breeding females ($\log y = -0{\cdot}04x + 0{\cdot}911$; d.f. 12, $P = 0{\cdot}05$) (Fig. 5).

Numbers

Numbers of deer mice on the control grids were low during May. Densities ranged from two to six individuals per grid. They increased in late June and continued to increase through July and August. Peak densities of sixteen to twenty-two individuals per grid were reached during late August and early September. The changes in the minimum number alive were very similar on all five grids (Fig. 6).

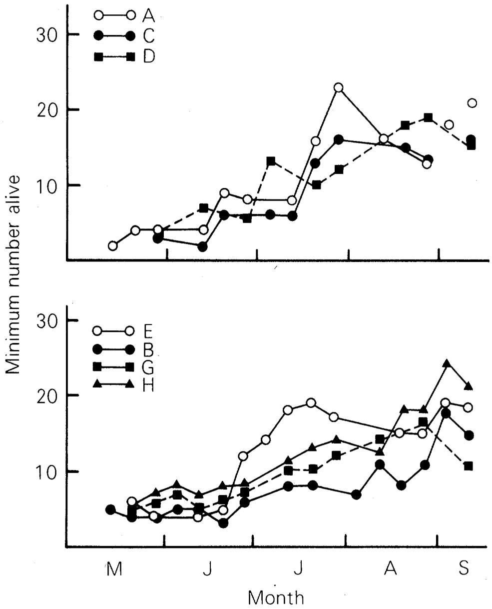

FIG. 6. Changes in population size (minimum number alive) on the experimental (A, E) and control (C, D, B, G, H) grids during 1983.

On the female removal grids, the initial number of deer mice was similar to the control grids. In grids A, the two resident breeding females were caged on 16 June. In grid E the two resident breeding females were removed on 23 June.

In late July, the number of deer mice on grid A increased to 1·5–3 times control densities. During August, numbers declined to the level of the control grids. Similarly, numbers on grid E resembled those on the controls during May and June. However, they increased during late June and early July to 1·6–3 times higher than numbers in the control grids. During late July, this population also declined to the level of the control grids.

In summary, densities were 1·5–3 times higher on the female removal grids (A, E) than on the control grids during late July. Thereafter, numbers in the experimental grids remained relatively constant whereas numbers in the control grids increased slowly. By the end of the trapping season in September, densities were very similar on most grids.

Movements between grids

Adult males were highly mobile and spent less time as residents in the live-trapping grids than females. From fifty-one adult males caught in all the live-trapping grids, 65% were caught for only one or two sessions. In spite of the distances between grids, 22% of the adult males were caught on more than one grid. Most of these movements (90%) occurred during the breeding season. In contrast, females spent more time as residents and moved little between grids. From twenty-three adult females caught, 35% were caught for less than two sessions. Only one adult female moved between two grids and this movement took place outside the breeding season.

Among juveniles, from a total of 195 juveniles live-trapped on all grids, 10% were caught on more than one grid. No sex bias in these movements was evident.

In the 3 years of study, there were eight instances where groups of two or three juveniles disappeared from a grid and, in the same trapping session and appeared later on a different grid. Juveniles in these groups had been ear-tagged in the same trapping session. The composition of the groups was variable. There were all female groups, all male groups and mixed groups. It is very likely that these are related individuals that moved together.

Migration

Migration was monitored by continuously removing animals that moved into two snap-trapping grids (X, Y). On grid X, a total of eighty-eight individuals were caught from May to September (3920 trap-nights). Most adult individuals (79%) were caught during May and June (breeding dispersal) and there was a strong sex bias towards males (Gadj = 14·51, d.f. 1, $P < 0{\cdot}001$). From twenty-seven adults caught during these 2 months 85% were males.

On grid Y, a total of ninety-six individuals were caught (3920 trap-nights). Like grid X, most adult individuals (79%) were caught during May and June, and the sex ratio was also skewed towards males (Gadj = 5·36, d.f. 1, $P < 0{\cdot}025$). From twenty-three adults caught during these 2 months 74% were males.

Most juveniles (94%) arrived on these grids when they were over 16 g (natal dispersal) (Fig. 3). Only two juveniles under 15 g were caught. Juveniles began moving onto grid X from 21 July to September (Fig. 7). The sex ratio of juveniles ($n = 54$) was skewed towards females (57%), but the difference was not significant (Gadj = 1·17, d.f. 1, $P > 0{\cdot}05$).

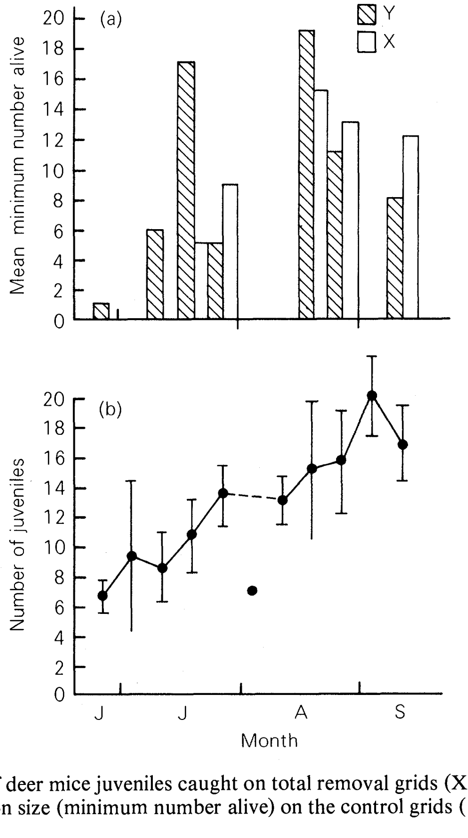

FIG. 7. (a) Number of deer mice juveniles caught on total removal grids (X, Y) in 1983. (b) Mean population size (minimum number alive) on the control grids (±1 S.D.).

On grid Y, juveniles were trapped from 28 June to September. Juveniles moved into this grid 3 weeks earlier than to grid X (Fig. 7). The most likely reason for this difference is the location of the grids. Grid X was in the lower part of a north-facing slope. Here the snow took longer to melt, delaying the entire season. The number of juveniles moving into grid Y showed two peaks: late July and August. The sex ratio of juveniles ($n = 67$) was skewed towards males, but the difference was not significant (Gadj = 0·72, d.f. 1, $P > 0{\cdot}25$).

During the breeding season (May–July), there were three times as many adults caught on total removal grids as on the controls (*t*-test, d.f. 5, $P < 0{\cdot}001$). The sex ratio was similar on removal and control grids (Gadj = 0·02, d.f. 1, $P > 0{\cdot}5$). Therefore, adult individuals are either attracted to areas where no other adults live or are prevented from settling in areas with resident individuals. In any case, both males and females show a similar tendency.

In terms of juveniles, the average number caught per trapping session on the total removal grids (10·2 ± 1·6 S.E.) was higher than on the controls (2·8 ± 1·1 S.E.). There were also three times as many juveniles caught on these grids as on the controls (sixty-one per removal grid, twenty-three per control grid). There was no significant departure from a 1:1 sex ratio among the juveniles.

The total number of juveniles caught in the total removal grids was also higher (1·2–1·7 times) than on the female removal grids (*t*-test, d.f. 2, $P < 0{\cdot}05$). As with adult individuals there seems to be a high number of potential recruits that do not establish on control areas.

DISCUSSION

The results of this study support the hypothesis that breeding females exert a negative influence on juveniles. Higher recruitment of juveniles occurred in both grids where breeding females were removed or caged after they had weaned their first litter. The higher recruitment to experimental grids resulted from an increase in the survival of resident juveniles. Once juveniles joined the trapable population their survival was not different from that on control areas. Therefore, it seems that interactions occur during the 3 weeks between the time juveniles are born and their recruitment into the trapable population. We do not know the nature of this negative interaction. Breeding females may (a) kill non-related offspring, or (b) influence dispersal of both their own and non-related offspring. In addition, females may have an indirect effect since males show more aggression in their presence than in their absence (Dewsbury 1984). Our results suggest that juveniles die *in situ* since the removal of females resulted in higher recruitment of juveniles of 15 g or less. The data from the total removal areas showed that these small individuals are not dispersing successfully.

The removal of females resulted in the disappearance of most adult males. The absence of adults of both sexes might have contributed to the higher recruitment on the experimental grids. However, we did not find a relationship between the number of males present during the breeding season on control grids and juvenile recruitment. In the female removal areas the only remaining adult male stayed in grid A where females were caged. This suggests that the distribution of males during the breeding season is strongly determined by the presence of females (Boonstra 1977).

The recruitment of first-litter juveniles was lower on grid A than on E. We do not understand what caused this difference. In these experiments the time when the selective removals take place is crucial. Removing breeding females too early may result in the loss of unweaned offspring. If the removal is done too late, the critical interactions may have occurred already. We chose as a removal date the day when juveniles were first live-trapped. In this way, we were certain that some first-litter juveniles were already weaned. However, since females differ in the day they give birth, their removal at the same time may account for the loss of some litters.

If breeding females affect dispersal, then there should be a pulse of animals moving into the total removal grids during the breeding season (late–June and July). A high number of juveniles moved into removal grid Y in July. Removal grid X did not show this increase; dispersal of juveniles was delayed on this grid as explained above. There was a considerable amount of dispersal after the breeding season had ended. This suggests that factors other than social interactions are important in the migration of juvenile individuals later in the season. In contrast to breeding dispersal, natal dispersal was not sex biased.

Petticrew & Sadleir (1974) proposed that adult males were responsible for the low recruitment of juveniles during the breeding season. Sadleir (1965) and Healey (1967) showed a seasonal rise and fall in male aggression related to the breeding season. Flowerdew (1974) removed adult males from a population of *Apodemus sylvaticus* and increased juvenile survival and immigration. Male-biased migration during the breeding season has been interpreted as a result of exclusion by dominant males (Fairbairn 1977). Mihok (1979) found a lower recruitment of juveniles during the second year of his study of a subarctic population of deer mice. He attributed this to the higher number of breeding males during the second year (3 *v.* 1). However, the density of breeding females in Mihok's study was also twice as high as in the first year. Therefore, lower recruitment might also be attributed to the higher number of females.

There is evidence from laboratory studies suggesting that breeding females could also be responsible for the low recruitment of juveniles during the breeding season. A cycle of aggression in pregnant and lactating females has been documented for *Peromyscus leucopus* (Gleason, Michael & Christian 1980) and *Peromyscus maniculatus* (Ayer & Whitsett 1980). Savidge (1974a,b) suggested that aggressive mothers may drive their offspring from the natal site when a subsequent litter is born. Recently, Wolff (1985) has shown that infanticide of non-related offspring by adults of both sexes is common in both *Peromyscus maniculatus* and *P. leucopus*. In his laboratory study, he found that maternal aggression prevented infanticide by strange adults.

In addition, there is indirect evidence from natural populations suggesting that females could have an important effect on population dynamics. Metzgar (1971, 1979) found that home ranges of resident adults (*Peromyscus leucopus*, *P. maniculatus*) of both sexes overlapped little with other individuals of the same sex. This tendency was stronger for females than for males. He suggested that this spacing out of home ranges imposed an upper limit on female numbers. Kondo (1977) found in *Apodemus speciosus* that only the females had mutually exclusive home ranges. He also found a negative relationship between the number of resident females and the number of female immigrants. He suggested that resident females prevented the settling of immigrant females (Kondo 1982). Fordham (1971) added supplemental food to a population. In response, females increased nearly 2·5 times while males were not influenced. He proposed that the sexes are regulated in different ways and that females may affect juvenile survival more than males. Hansen & Batzli (1978) found a negative relationship between adult female densities (*P. leucopus*) and adult survival, but no relationship to male densities. Furthermore, they found a positive (non-significant) relationship between dispersal of young and female densities. They suggested that aggressive behaviour by adult females limits densities in the spring and summer by influencing juvenile dispersal. Taitt (1981) found that both sexes increased after food addition, but females responded faster. She also found that juvenile survival was negatively related to the number of lactating females and unrelated to the number of breeding males.

In summary, these studies suggest that both sexes could potentially influence population dynamics. If both sexes exhibit spacing behaviour there are two possibilities. First, males and females may space themselves out with respect to individuals of similar sex (Redfield, Taitt & Krebs 1978a). Second, thay may space themselves out regardless of sex (Redfield, Taitt & Krebs 1978b). On the other hand, only one sex (either males or females) may exhibit spacing behaviour. Populations of deer mice in the Yukon seem to behave in the latter way. Females established residence in the grids with non-overlapping home ranges. A few males stayed on one grid throughout the season, but most males were very mobile. This was shown by both the live-trapping grids and the total removal grids. The most common mating system in these northern *Peromyscus* populations seems to be a non-defence polygyny (Dobson 1984). The low densities and large home ranges of females may place male territoriality under the threshold of economic defendability.

During the breeding season, juveniles may either die or disperse as a result of their interaction with adults. Adult males may behave aggressively towards male juveniles which may be potential competitors for mates. This is an unlikely possibility in our study area since juveniles do not reach sexual maturity during their first year. On the other hand, adult females may act aggressively towards unrelated juveniles that may compete with their own offspring. They may also cause their own offspring to disperse to conserve resources for raising subsequent litters (Savidge 1974a).

These interactions would result in higher mortality (Sadleir 1965; Healey 1967; Flowerdew 1974; Boonstra 1978; Taitt & Krebs 1981), increased emigration (Beacham 1979) and lower immigration (Redfield, Taitt & Krebs 1978a) of juveniles. In this study we have shown that breeding females affect juvenile recruitment. Adult males in turn, may also have an effect if infanticide in the field is as common as Wolff (1985) has shown in the laboratory.

Recent experimental studies have shown the relevance of female behaviour to population dynamics among small mammals (Redfield, Taitt & Krebs 1978a,b; Boonstra & Rodd 1983; Hansen & Nixon 1985; Gipps *et al.* 1985; this study). Further studies should look at the relative importance and interaction between the sexes as has been done in microtine studies (Redfield, Taitt & Krebs 1978a,b; Boonstra & Rodd 1983). The main technique used so far is selective removal, but there are two main problems with this. Firstly, removal of one sex may affect the other (as in this study). Secondly, removal of females could result in the loss of unweaned or subsequent litters. The use of semipermeable cages seems to alleviate both problems. However, since juveniles are protected, it removes other possible sources of early mortality. In addition, females are provided with higher quality food and this may influence their offspring.

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REFERENCES

Ayer, M. L. & Whitsett, J. M. (1980). Aggressive behavior of female prairie deermice in laboratory populations. *Animal Behaviour*, **28,** 763–771.

Beacham, T. D. (1979). Size and growth characteristics of dispersing voles, *Microtus townsendii. Oecologia*, **42,** 1–10.

Boonstra, R. (1977). Effects of conspecifics on survival during population declines in *Microtus townsendii. Journal of Animal Ecology*, **46,** 835–851.

Boonstra, R. (1978). Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. *Ecology*, **59,** 136–148.

Boonstra, R. & Rodd, H. (1983). Regulation of breeding densities in *Microtus pennsylvanicus. Journal of Animal Ecology*, **52,** 757–780.

Dewsbury, D. A. (1984). Aggression, copulation and differential reproduction of deer mice (*Peromyscus maniculatus*) in a semi-natural enclosure. *Behaviour*, **91,** 1–23.

Dobson, F. S. (1984). Environmental influences on sciurid mating systems. *The biology of ground squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 229–249. University of Nebraska Press, Nebraska.

Fairbairn, D. J. (1977). The spring decline in deer mice: death or dispersal? *Canadian Journal of Zoology*, **55,** 84–92.

Flowerdew, J. R. (1974). Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (*Apodemus sylvaticus*). *Journal of Animal Ecology*, **43,** 499–510.

Fordham, R. H. (1971). Field populations of *Peromyscus* with supplemental food. *Ecology*, **52,** 138–146.

Galindo, C. & Krebs, C. J. (1985). Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. *Canadian Journal of Zoology*, **63,** 1870–1879.

Gilbert, B. S. & Krebs, C. J. (1981). Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia*, **51,** 326–331.

Gilbert, B. S. & Krebs, C. J. (1984). Competition between *Peromyscus maniculatus* and other small rodents in the boreal forest of the southern Yukon. *Acta Zoologica Fennica*, **172,** 51–56.

Gipps, J. H. W., Flynn, M. P., Gurnell, J. & Healing, T. D. (1985). The spring decline in populations of the bank vole. *Clethrionomys glareolus*, and the role of female density. *Journal of Animal Ecology*, **54,** 351–358.

Gleason, P. E., Michael, S. D. & Christian, J. J. (1980). Aggressive behavior during the reproductive cycle of female *Peromyscus leucopus*: the effect of encounter site. *Behavioral and Neural Biology*, **29,** 506–511.

Hansen, L. P. & Batzli, G. O. (1978). The influence of food availability on the white-footed mouse: populations on isolated woodlots. *Journal of Mammalogy*, **60,** 335–342.

Hansen, L. P. & Nixon, C. M. (1985). Effects of adults on the demography of fox squirrels (*Sciurus niger*). *Canadian Journal of Zoology*, **63,** 861–867.

Healey, M. C. (1967). Aggression and self-regulation of population size in deermice. *Ecology*, **48,** 377–392.

Kondo, T. (1977). Social behavior of the Japanese wood mouse *Apodemus speciosus* (Temminck et Schlegel), in the field. *Japanese Journal of Ecology*, **27,** 301–310.

Kondo, T. (1982). A population study of the Japanese wood mouse *Apodemus speciosus* (Mammalia: Muridae), with reference to its social behavior. *Researches in Population Ecology*, **24,** 85–96.

Metzgar, L. H. (1971). Behavioral population regulation in the woodmouse *Peromyscus leucopus. American Midland Naturalist*, **86,** 435–447.

Metzgar, L. H. (1979). Dispersion patterns in a *Peromyscus population. Journal of Mammalogy*, **60,** 129–145.

Mihok, S. (1979). Behavioral structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus maniculatus. Canadian Journal of Zoology*, **57,** 1520–1535.

Millar, J. S. (1982). Life cycle characteristics of northern *Peromyscus maniculatus borealis. Canadian Journal of Zoology*, **60,** 510–515.

Petticrew, B. G. & Sadleir, R. M. F. S. (1974). The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Population dynamics. *Canadian Journal of Zoology*, **52,** 107–118.

Redfield, J. A., Taitt, M. J. & Krebs, C. J. (1978a). Experimental alteration of sex ratios in populations of *Microtus townsendii,* a field vole. *Canadian Journal of Zoology*, **56,** 17–27.

Redfield, J. A., Taitt, M. J. & Krebs, C. J. (1978b). Experimental alteration of sex ratios in populations of *Microtus oregoni*, the creeping vole. *Journal of Animal Ecology*, **47,** 55–69.

Rowley, M. H. & Christian, J. J. (1976). Intraspecific aggression of *Peromyscus leucopus. Behavioral Biology*, **17,** 249–253.

Sadleir, R. M. F. S. (1965). The relationship between agonistic behaviour and population changes in the deermouse *Peromyscus maniculatus* (Wagner). *Journal of Animal Ecology*, **34,** 331–352.

Savidge, I. R. (1974a). Social factors in dispersal of deer mice (*Peromyscus maniculatus*) from their natal site. *American Midland Naturalist*, **91,** 395–405.

Savidge, I. R. (1974b). Maternal aggressiveness and litter survival in deer mice (*Peromyscus maniculatus bairdi*). *American Midland Naturalist*, **91,** 449–451.

Sexton, O. J., Douglass, J. F., Bloye, R. R. & Pesce, A. (1982). Thirteen-fold change in population size of *Peromyscus leucopus*. *Canadian Journal of Zoology*, **60,** 2224–2225.

Sullivan, T. P. (1977). Demography and dispersal in island and mainland populations of deer mouse, *Peromyscus maniculatus*. *Ecology*, **58,** 964–978.

Sullivan, T. P. & Krebs, C. J. (1981). An irruption of deer mice after logging of coastal coniferous forest. *Canadian Journal of Forestry Research*, **11,** 586–592.

Taitt, M. J. (1981). The effect of extra food on small rodent populations: I. Deermice (*Peromyscus maniculatus*). *Journal of Animal Ecology*, **50,** 111–124.

Taitt, M. J. & Krebs, C. J. (1981). The effect of extra food on small rodent populations: II. Voles (*Microtus townsendii*). *Journal of Animal Ecology*, **50,** 125–137.

Terman, C. R. (1968). Population dynamics. *Biology of* Peromyscus (*Rodentia*) (Ed. by J. A. King), Special Publications No. 2, American Society of Mammalogists,

Wolff, J. O. (1985). Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. *Animal Behaviour*, **33,** 117–121.

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