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EFFECTS OF ADULT MEADOW VOLES, *MICROTUS PENNSYLVANICUS*, ON YOUNG CONSPECIFICS IN FIELD POPULATIONS

BY F. HELEN RODD AND RUDY BOONSTRA

*Division of Life Sciences, Scarborough Campus, University of Toronto,
1265 Military Trail, Scarborough, Ontario, Canada M1C 1A4*

SUMMARY

(1) We investigated the influence of *Microtus pennsylvanicus* adults on young conspecifics by manipulating the density or sex ratio of the adult segment of several experimental populations.

(2) Adults were removed from four experimental grids as follows: (i) all breeding males (female grid); (ii) all breeding females (male grid); (iii) most adults throughout the autumn, winter and spring (autumn-removal grid); and (iv) most adults throughout the spring (spring-removal grid). All manipulations were repeated the following year.

(3) Survival, ages at sexual maturity, and reproductive rates were significantly improved in young individuals, especially young females, on all experimental grids except the female grid. The demography of young animals on the female grid was either similar to that on the control grid or intermediate between that on the control grid and that on the other experimental grids. For young females, there was a significant, negative relationship between adult density and each of these parameters; for young males, only survival rates of very young animals were negatively related to adult density. Individual growth rates were not influenced by any of the manipulations.

(4) Therefore, adult animals, especially adult females, play a major role in limiting the density and fitness of young individuals.

INTRODUCTION

Higher animals have evolved behavioural and physiological mechanisms, such as territoriality and pheromones, that limit population density (Ebling & Stoddart 1978; Tamarin 1980; Sibly & Smith 1985; Haigh 1987). Certain social and age classes are more susceptible to these types of regulation than other groups of individuals (Dunbar 1985; Watson 1985). Young, subordinate animals are good targets for suppression; not only are they vulnerable, but slight changes in juvenile survival and maturation can produce profound changes in a population's demography (Cole 1954; Lewontin 1965; Krebs 1966, 1971; Christian 1971; Gaines & Rose 1976). Adults do play an important role in influencing the basic parameters of juveniles' lives in many small mammals, e.g. they affect survival and reproduction in *Peromyscus* (Sadleir 1965; Healey 1967; Haigh 1987); survival and reproduction in *Spermophilus* (Slade & Balph 1974); reproduction in *Mus*, (Vandenbergh 1987); survival and reproduction in *Microtus* (Boonstra 1978); survival in *Lepus* (Boutin 1984); survival in *Sciurus* (Hansen & Nixon 1985).

We explored the effects of the density and composition of the adult portion of a meadow vole (*Microtus pennsylvanicus* (Ord)) population on juvenile life-history traits. The relative importance of adult males and adult females to population regulation had been debated with increasing evidence that, in some species, females play the major role (Bujalska 1973; Boonstra 1978; Redfield, Taitt & Krebs 1978). Therefore, our manipulations were chosen to look at both the effects of total adult density and the independent influence of adults of each sex on young animals. We concentrated on the early part of the breeding season, when interaction rates are high (Turner & Iverson 1973), breeding activity is maximal, and young first appear in the population.

MATERIALS AND METHODS

This study was done on a 10-ha grassland adjacent to the Pearson (formerly Toronto) International Airport. The dominant grass species were *Poa pratensis* L., *Poa compressa* L., *Agropyron repens* (L.), *Festuca pratensis* Hudson, and *Bromus inermis* Leyss. Other plants included *Melilotus officinalis* (L.), *Medicago lupulina* L., *Geum macrophyllum* Willd., *Solidago* spp., and *Aster* spp. Small mammals on the grids were *Microtus pennsylvanicus* (meadow vole), *Peromyscus maniculatus bairdii* (Wagner) (deer mouse), and *Mus musculus* L. (house mouse). Boonstra & Rood (1983) give further details on the area.

Each of the five 0.7-ha grids had 100 trap points spaced 7.6 m apart in a 10 × 10 pattern and was at least 30 m from any adjacent grid. One or two Longworth live-traps, depending on the population density, were placed at each trap station and were protected by a small, wooden shelter (Iverson & Turner 1969). From May to November, pitfall traps (Boonstra & Krebs 1978) were also used on the control grid. Traps were baited with oats and provided with cotton for bedding.

We trapped for one day and two nights every second week, weather permitting. Traps were set in the afternoon, checked the following morning, again in the afternoon, and a third time the next morning. To avoid trap-induced mortality, we set traps only at night during the summer and only for one night in severe winter weather. Each vole was ear-tagged when first caught and its weight, sex, breeding condition, tag number, and location on the grid were recorded at each capture.

In addition to monitoring a control grid, we manipulated the adult populations on four experimental grids. The grids were arranged in a roughly linear pattern as follows: control, male, female, autumn-removal and spring-removal (Boonstra & Rodd 1983). All breeding females were continuously removed from the male grid. All breeding males were continuously removed from the female grid. On the autumn-removal grid, the population was monitored for at least one trapping session in the autumn; on subsequent sessions, all but fifty selected animals were removed. The fifty animals that were allowed to remain on the grid were young of the year that had not yet produced. Body weight was used as an index of age in cases where an individual's reproductive history was unclear. The sex ratio of resident animals was maintained at approximately 1:1. Animals trapped on the periphery of the grid were removed to form a buffer zone between the animals on the grid and those on the surrounding land. Immigrants (untagged individuals) were removed as they were captured. Just before the start of the breeding season, in early spring, population size was further reduced to about thirty-five individuals by removing randomly selected animals. With the start of the breeding season, all new young animals

(< 34 g) were assumed to be offspring of the grid's residents; they were tagged and allowed to remain.

The population on the spring-removal grid was monitored in the autumn (except in the first trial, when trapping did not begin until March 1979), whenever weather permitted during the winter, and in the spring. All but thirty-five animals were removed in the spring, just before the start of the breeding season. These animals were chosen randomly from among those resident individuals which had histories comparable with those left on the autumn-removal grid. Consequently, animals that remained on the spring-removal grid had been caught the previous autumn and, at that time, were immature young of the year. All large animals (> 33 g) moving into the grid after cropping began, and those on the periphery of the grid, were removed. As on the autumn-removal grid, new, young animals, which we assumed had been born on the grid, were left on it. In the first year, numbers on this grid were low, so all individuals were allowed to remain on the area.

Two complete trials of the experiment were done. The control grid was trapped continuously from 4 July 1978 throughout the study. The male and female grids were trapped from 4 July 1978 to 22 November 1978, from 29 March 1979 to 23 November 1979, and from 26 March 1980 to 21 November 1980. The autumn-removal grid was trapped from 10 October 1978 to 6 July 1979, the spring-removal grid from 14 March 1979 to 6 July 1979, and both autumn- and spring-removal grids from 26 September 1979 to 4 July 1980. The analyses done here include the data gathered from 14 March to 6 July 1979 (Trial 1) and 12 March to 4 July 1980 (Trial 2).

As live microtine rodents are difficult to age accurately (Krebs & Myers 1974), we used weight as an index of the animal's age. Animals were classified as adult (> 33 g), subadult (22–33 g), or juvenile (< 22 g). They were judged to be in breeding condition, in males, by the presence of scrotal testes and, in females, by the presence of a perforate vaginal orifice, lactation tissue, or a litter. They were classified as sexually mature if any of these criteria were met or, in females, if they had a widely separated pubic symphysis.

RESULTS

Trappability

The minimum trappability (Krebs & Boonstra 1984) for all populations in the spring and summer was at least 70%, with the exception of the autumn- and spring-removal populations in Trial 2 (trappability of 56%).

Population density

Population densities just prior to and during the study period, as estimated by the Jolly procedure (Jolly & Dickson 1983), are shown in Fig. 1. In Trial 1, all five populations experienced a severe decline, which began in early January 1979. At that time, freezing rain replaced the snow cover with a layer of ice and very low temperatures followed. In March and April, when the weather improved, numbers on the control grid continued to decline because of emigration (Boonstra & Rodd 1983; Boonstra 1985). In Trial 2, numbers on the control rose throughout the winter (1979–80) but declined at the onset of the breeding period to a low in May. In both trials, once the manipulations were begun, the experimental population densities were maintained at lower densities than those on the control grids, despite immigration into the manipulated populations. On the male

FIG. 1. Changes in population size as estimated by the Jolly procedure for (a) Trial 1 [Feb.–July 1979] and (b) Trial 2 [Feb.–July 1980] for control (■) and experimental grids: male (○), female (●), autumn-removal (△) and spring-removal (▲). (See Boonstra & Rodd (1983), Rodd & Boonstra (1984), Boonstra (1985) for a complete description of population densities.)

grid, each spring, in both trials, the experimental removal of females in breeding condition resulted in an immediate decline in the number of breeding males (Boonstra & Rodd 1983). In Trial 1, adult male numbers fell to 35% of the control level in May, but by June returned, as the young of the year matured, to levels found on the control. The pattern was similar in Trial 2 but there the numbers fell only to 65% of control levels in May. On the female grid in Trial 1, the numbers of breeding females were slightly lower than on the Control grid. On the autumn- and spring-removal grids, densities of adults of both sexes were maintained at levels lower than on the control.

Survival rates

We used two indices to estimate juvenile survival. The first index estimates survival of young voles from birth to first capture (some time after 14–18 days old). It was calculated for the study's major recruitment period (early May until the end of the study in early July) by dividing the number of young voles (< 30 g) by the number of females lactating 4 weeks previously (Krebs & Delong 1965). It could not be calculated for the male grid because all breeding females were removed from that grid. This index was higher in both trials for the autumn- and spring-removal grids than for the control grids (Table 1). For the female grid, it was higher than for the control grid in Trial 1 but lower in Trial 2.

A large early juvenile survival index may indicate good juvenile survival, but it may also indicate low juvenile growth rate, large litter size, good trappability and/or a large influx of young animals. Each of these potentially biasing factors will be examined to determine its effect on the index.

Growth rate could not have affected this index, as analyses showed no differences between experimental and control animals (see below). Litter size could only have been

TABLE 1. Index of early juvenile survival, expressed as the number of young *Microtus pennsylvanicus* recruited per lactating female for the recruitment period (May–July), with the total number of lactating females caught in parentheses

Grid	Trial 1	Trial 2
Control (live-traps only)	1.4 (88)	0.9 (208)
Control (live-traps plus pitfall traps)	1.7 (94)	—
Male	—	—
Female	3.1 (26)	0.7 (169)
Autumn-removal	2.3 (55)	1.2 (58)
Spring-removal	3.5 (14)	1.2 (72)

significantly affected, in a way that would bias the index, by female body weight (Frank 1957; Krebs & Myers 1974). Unfortunately, few data on litter size were available from this study. However, since litter size may increase with maternal size (Keller 1985) and there were more large females on the control grids than on the experimental grids, this bias would reduce the differences between the control and experimental indices.

Juveniles may enter traps at a younger age when adult males have been removed from the population (Watts 1970a). This increase in trappability may cause an apparent increase in the index of their survival rates and would bias the results. Maximum live-trap trappabilities of voles weighing less than 30 g did not differ among the grids. There were also no differences among the grids in Trial 1 for age (weight) at first capture. However, to ensure that there was no bias against the control grid, we included the information on voles caught in the pitfall traps on that grid, since pitfall traps tend to capture animals at a younger age than live-traps (Boonstra & Rodd 1984). Despite the addition of these data, the index remained low for the control grid in Trial 1 (Table 1). In Trial 2, animals on the control grid were entering live-traps for the first time at a significantly lower weight than on the other grids (unpublished data), so pitfall trap data were not used. Therefore, differences in trappability were not responsible for differences in the index of early juvenile survival.

Finally, it was impossible to distinguish between young voles that had wandered on to the grid and those that had been born there. Because of lower densities, immigration rates were probably higher on to experimental grids than on to the control grid, and this may account for some of the differences between their index values. Since the litter size and trappability biases were generally acting to reduce differences between experimental and control populations, we assume that these factors cancel one another's effect to some extent. Therefore, the manipulations appear to have improved juvenile survival on all experimental grids, except the female grid in Trial 2.

A multiple regression analysis was done where the dependent variable was the mean index of early juvenile survival for all grids except the male grid in both trials, and the independent variables were the mean densities of male and female breeding adults during the spring and early summer (Sokal & Rohlf 1981). It showed a significant, negative relationship between the density of breeding adults and early juvenile survival (Table 2).

Our second index estimated survival from an animal's first capture until the end of the trial period. Since most young began entering the trappable populations in May and June, and the trial ended during the first week of July, all could theoretically have lived until the end of the trial. The index was calculated for each young animal, using the actual length of

time that it was present on the grid as a proportion of the time it could theoretically have lived there:

$$\text{Individual Score} = \frac{\text{actual life span}}{\text{potential life span}} \\ = \frac{(\text{time of last capture} - \text{time of first capture})}{(\text{end of trial} - \text{time of first capture})}.$$

In Trial 1, there were no differences between control and experimental grids either for males or females (Table 3); in Trial 2, there were no differences for males but there were for females ($\chi^2 = 27.8$, $P < 0.0001$) (Kruskal-Wallis, SPSS Inc. 1983). Pairwise comparisons among the grids in Trial 2 showed that female survival rates were similar on the control and female grids and that rates on those grids were significantly lower than those on the male, autumn-removal and spring-removal grids (Lee-Desu statistic, Survival procedure, SPSS Inc. 1983). This suggests that adults, especially adult females, play a role in reducing the survival rates of young females. It is interesting to note that the index was higher for females than males on every grid in both trials.

Multiple regression analysis (as above) showed no significant relationship between adult density and mean survival scores for either females or males.

Individual growth rates

Growth rates of young animals (< 34 g) were determined for the early part of the breeding season, from mid-March to early July. Instantaneous growth rates per day were

TABLE 2. Multiple regression analyses with mean scores for a given analysis (see text) for all grids in both trials as the dependent variable, and the mean densities of male and female breeding adults during the spring-early summer period as the independent variables. *F*-values are shown in brackets. Sample sizes for all analyses are ten, except for the index of early juvenile survival index ($n = 8$)

Dependent variable	Standard partial regression coefficients (<i>b</i>)		Coefficient of multiple determination (R^2) ^b
	Adult female density ^a	Adult male density ^a	
Early juvenile survival	-0.93 N.S. [4.2]	0.09 N.S. [0.0]	(-) 0.74* [7.0]
Late juvenile-subadult survival			
Female	-0.79 N.S. [5.0]	0.12 N.S. [0.1]	(-) 0.51 N.S. [3.6]
Male	-0.05 N.S. [0.0]	0.14 N.S. [0.0]	(+) 0.01 N.S. [0.0]
Proportion mature			
Female	-0.72*** [32.7]†	-0.33** [6.8]†	(-) 0.94*** [52.1]
Male	-0.64 N.S. [2.3]	0.19 N.S. [0.2]	(-) 0.28 N.S. [1.4]
Weight at sexual maturity			
Female	0.64*** [23.9]†	0.41* [9.6]†	(+) 0.93*** [47.1]
Male	0.50 N.S. [1.2]	-0.46 N.S. [1.0]	(-) 0.16 N.S. [0.6]

† No difference between values of *b* for adult male and adult female densities.

^a d.f. = 1, 7 (1, 5 for early juvenile survival).

^b d.f. = 2, 7 (2, 5 for early juvenile survival).

N.S. $P > 0.05$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

TABLE 3. Mean survival index of young voles. The index is calculated as the actual length of time that each animal was present on the grid as a proportion of the time it could theoretically have lived there

Trial	Grid	Males (<i>n</i>)	Females (<i>n</i>)
1	Control	0.34 (78)	0.62 (77)
	Male	0.30 (20) N.S.	0.87 (16) N.S.
	Female	0.36 (34) N.S.	0.60 (32) N.S.
	Autumn-removal	0.30 (40) N.S.	0.65 (46) N.S.
	Spring-removal	0.51 (28) N.S.	0.68 (19) N.S.
2	Control	0.46 (163)	0.47 (149)
	Male	0.29 (23) N.S.	0.67 (15)*
	Female	0.26 (37) N.S.	0.50 (59) N.S.
	Autumn-removal	0.42 (35) N.S.	0.79 (38)*
	Spring-removal	0.43 (45) N.S.	0.76 (60)*

N.S. $P > 0.05$.

* $P < 0.05$.

TABLE 4. Instantaneous individual growth rates per day for young voles (< 34 g) in the spring and early summer. Rates are adjusted to a standard weight (25 g) using the regression of instantaneous growth rate on body weight

Trial	Grid	Males (<i>n</i>)	Females (<i>n</i>)
1	Control	0.024 (48)	0.025 (83)
	Male	0.034 (7) N.S.	0.027 (15) N.S.
	Female	0.025 (16) N.S.	0.026 (27) N.S.
	Autumn-removal	0.020 (22) N.S.	0.025 (44) N.S.
	Spring-removal	0.021 (28) N.S.	0.021 (17) N.S.
2	Control	0.014 (119)	0.018 (124)
	Male	0.019 (10) N.S.	0.012 (5) N.S.
	Female	0.015 (12) N.S.	0.019 (42) N.S.
	Autumn-removal	0.014 (21) N.S.	0.018 (41) N.S.
	Spring-removal	0.022 (34) N.S.	0.018 (60) N.S.

N.S. $P > 0.05$.

calculated for individuals for each 2-, or at most 4-week capture interval during the period of interest. Body weight was used as a covariate in the analyses, since growth rates slow as animals increase in size. An initial analysis, using a two-way analysis of covariance (Nie *et al.* 1975; Beacham 1980), produced interactions between two factors, grid and sex, and between the factors and the covariate, weight. This meant that the assumption of homogeneity of slopes was violated. Thus, we had to simplify the analysis and group the data by sex for each trial. One-way analyses of covariance, with growth rate as the dependent variable and weight as the covariate, were done on each of the four data sets (SPSS Inc. 1983; Neter, Wasserman & Kutner 1985).

Pair-wise comparisons between grids for males and females in Trial 1, and females in Trial 2, were done with the Scheffé test (Neter, Wasserman & Kutner 1985). Individual growth rates did not differ between control and experimental grids for these groups (Table 4). There was a significant interaction between grid and weight in Trial 2 for young males but none of the experimental-control contrasts differed significantly.

TABLE 5. Percentage of young *Microtus pennsylvanicus* individuals (< 34 g) in reproductive condition during the early part of the breeding season (late March–early June). Numbers young voles known to be alive on the areas are in parentheses

Trial	Grid	Males	Females
1	Control	20 (88)	61 (89)
	Male	35 (31) N.S.	87 (31) N.S.
	Female	14 (48) N.S.	80 (45) N.S.
	Autumn-removal	13 (55) N.S.	71 (80) N.S.
	Spring-removal	35 (41) N.S.	81 (26) N.S.
2	Control	6 (215)	14 (203)
	Male	26 (47)*	58 (62)*
	Female	12 (73) N.S.	40 (74)*
	Autumn-removal	29 (59)*	68 (69)*
	Spring-removal	46 (52)*	67 (63)*

N.S. $P > 0.05$.

* $P < 0.05$.

Reproduction

Subadults may or may not attain maturity in the year of their birth, depending on the conditions, so we assessed the impact of our manipulations on subadult maturation. Breeding activity was determined by examining the external reproductive characteristics of young animals (< 34 g); males were mature if they had scrotal testes and females were mature if their vagina was perforate. All young animals were followed until the end of the trial period and were classified as either mature or immature.

In Trial 1, there were no differences, for males or females, among any of the grids (Table 5). Generally, a larger percentage of subadults were in reproductive condition in Trial 1 than in Trial 2, perhaps reflecting the lower population densities overall in Trial 1. In Trial 2, more of the young animals were breeding on all experimental grids than on the control grid, with the exception of males on the female grid (G -statistic; Sokal & Rohlf 1981). Among the experimental grids, the female grid showed lower proportions reaching maturity than on the autumn-removal grid for females and on the spring-removal grid for males. Therefore, adults, especially females, can have a considerable role in suppressing reproduction in young animals.

The multiple regression analysis showed a significant negative relationship between breeding adult density and the percentage of mature females (Fig. 2), with both adult females and adult males making a significant contribution to this relationship (Table 2). There was no significant relationship between adult density and the percentage of young males that became mature.

Age at sexual maturity

Median weights at sexual maturity were estimated using the probit technique of Leslie, Perry & Watson (1945) (Table 6). Individuals were classified as either having attained maturity or not (see Materials and Methods), and were placed in 4-g weight intervals according to body weight. Females in advanced stages of pregnancy were excluded from the analysis. Differences among grids were tested using maximum likelihood logistic regression (CATMOD, SAS Institute Inc. 1985).

Females on all experimental grids in both trials matured at significantly lower weights than did those on the control grids (Table 6). Comparisons among the experimental grids

FIG. 2. Relationship between numbers of breeding adults on all grids in the spring and early summer, and percentages of young females that were sexually mature (perforate vaginae) in Trial 1 (□) and Trial 2 (■). The numbers indicate grids: 1, control; 2, male; 3, female; 4, autumn-removal; 5, spring-removal.

showed no differences among grids in Trial 1; in Trial 2, females on the autumn-removal grid matured at significantly lower ($P=0.0004$) weights than did those on the female grid.

With the exception of a few individuals on the autumn- and spring-removal grids in Trial 2 that matured at lighter weights, males on all grids matured in the same weight range, and there were no significant differences among grids (Table 6). In Trial 2, none of the males on the control, male, or female grids in the 15–22 g range were sexually mature, but some of those on the autumn- (35%) and spring-removal (21%) grids were.

Since large, adult rodents inhibit subordinate individuals from entering traps (Kikkawa 1964; Summerlin & Wolfe 1973), these apparent reductions in weight at sexual

TABLE 6. Median weights at sexual maturity (with 95% confidence intervals)

Grid	Males [n]	Females [n]
Trial 1		
Control	31.4 (30.1–32.8) [96]	22.5 (20.0–25.3) [293]
Male	30.7 (29.2–32.3) [34] N.S.	10.5 (4.8–23.1) [10]**
Female	32.9 (31.3–34.5) [85] N.S.	11.9 (7.2–19.6) [56]*
Autumn-removal	31.3 (29.6–33.0) [52] N.S.	16.4 (14.1–19.0) [169]**
Spring-removal	31.9 (30.7–33.3) [76] N.S.	12.7 (7.4–21.9) [57]**
Trial 2		
Control	32.0 (30.8–33.3) [120]	30.2 (28.1–32.4) [362]
Male	30.9 (29.5–32.4) [70] N.S.	22.7 (19.4–26.5) [104]***
Female	31.9 (30.1–33.8) [72] N.S.	25.4 (23.5–27.4) [75]*
Autumn-removal	31.6 (30.4–32.8) [89] N.S.	18.7 (15.6–22.4) [201]***
Spring-removal	30.8 (29.4–32.2) [117] N.S.	21.4 (19.1–24.1) [224]***

N.S. $P>0.05$.

* $P<0.01$.

** $P<0.001$.

*** $P<0.0001$.

maturity may have been a result of improved trappability of small, mature individuals on the experimental grids. An analysis of the maximum trappabilities of mature animals in the 14–35 g range showed that females on experimental grids in Trial 1 were indeed more likely to be caught than were similar animals on the control grid. When trappabilities for animals on the control grids, including those caught in pitfall traps, were recalculated, the new trappabilities were similar to those for the experimental grids. Nevertheless, the addition of young caught in pitfalls to those caught in live-traps did not significantly change the estimate of the weight at sexual maturity on control grids. Thus, the relationships between the control and experimental weights at maturity remained the same. We conclude that the experimental manipulations significantly reduced the weight at sexual maturity for females but not for males.

Since growth rates did not differ between experimental and control grids, the fact that animals on the experimental grids were reaching sexual maturity at lower weights than those on the control grids means that the experimental animals were maturing at younger ages. A large proportion of the variability in weight at sexual maturity for females can be explained by the density of breeding adults with both adult females and adult males contributing to the delay in reproduction (Table 2). There was little variability in the weights at which young males matured, and adult densities did not explain a significant amount of what variability there was.

DISCUSSION

Survival rates

The survival analyses, although not all significant, do indicate the importance of adults in determining the survival rates of young animals (Tables 1–3). Their influence appears to be most substantial during the first few weeks of the voles' lives, especially for young males. Adults maintain their influence on young females well into subadulthood. Young animals had highest survival rates on the grids from which adult females, or adults of both sexes, had been removed. This suggests that females are more important than males in suppressing the survival of young animals.

For the second survival index, as well as for several other parameters examined here, differences between control and experimental grids were larger in Trial 2 than Trial 1. Although the overall population patterns on the control grids were similar for the 2 years, population densities and levels of strife (indicated by wounding levels) were higher during the second trial (Rodd & Boonstra 1984). As a result, density differences between control and experimental grids were greater in Trial 2 and improvements in survival and reproduction more obvious.

Other studies have shown that adult females, specifically, have a significant impact on juvenile survival. As in Trial 2, young animals may not survive better on male-removal grids than on control grids (Watts 1970a; Boonstra 1978; Porter & Dueser 1986). However, young do survive better on grids from which adults of both sexes have been removed (Smyth 1968; Krebs, Keller & Tamarin 1969; Boonstra 1977, 1978; this study) or from which adult females have been removed (Redfield, Taitt & Krebs 1978; Gilbert *et al.* 1986; this study). In both experimental and unmanipulated populations, negative relationships between female density and juvenile survival have been found (Boonstra 1978; Redfield, Taitt & Krebs 1978; Getz *et al.* 1979); there was no evidence of a

significant relationship between male density and juvenile survival in any of those studies (however, see Beacham 1979a).

In a polygamous species like *M. pennsylvanicus*, where the males provide no care of the young, it may be difficult for males to identify their own offspring, and since it is not to a male's advantage to hamper the survival or reproduction of his kin, the best strategy may be to play little or no role in limiting the survival of young, immature animals. Laboratory behavioural studies on *M. pennsylvanicus* showed that some females were very aggressive towards young animals but adult males were largely inquisitive (Boonstra 1984). In small outdoor breeding enclosures, the presence of any male, including the father, had no effect on the litter's survival, but maternal behaviour accounted for as much as 50% of the variance among mothers in mean number of offspring recruited per litter (Anderson 1975).

In non-microtines, laboratory studies have shown that adults can be very aggressive towards juveniles and that these interactions can be fatal (Sadleir 1965; Terman 1965; Healey 1967). Therefore, it is possible that adult voles actually kill young ones but since small voles are more likely to disperse than larger ones (Krebs *et al.* 1976; Beacham 1981; Nadeau, Lombardi & Tamarin 1981; however, see Myers & Krebs 1971; Tamarin 1977), adults may also be reducing survival rates by forcing young voles to emigrate.

Adults may affect juvenile survival more subtly by inhibiting their access to food and cover. Juvenile survival rates have been improved by the addition of food (Krebs & Delong 1965) and possibly improved by the addition of cover (Taitt *et al.* 1981).

Individual growth rates

Beacham (1979b) predicted that removal of the largest overwintered voles would increase average individual growth rates because he found that fast-growing voles experienced more social pressure to disperse than similar-sized individuals that grew more slowly. Also, there are indications from field populations that growth rates of juveniles are reduced at high densities (Christian 1971; Koshkina & Korotkov 1975). This led us to expect increased growth rates for the young animals on the manipulated grids. However, there were no significant differences in growth rates between control and experimental grids, perhaps because the data were often variable and, in some cases, the sample sizes were small (Table 4).

Studies on other species have shown that adults can reduce growth rates in young animals (Myllymäki 1974 (cited in Myllymäki 1977); Boonstra 1978). However, as in our study, Porter & Dueser (1986) were unable to increase *M. pennsylvanicus* subadult male growth rates by removing adult males. A possible explanation is that growth rates in this species are not influenced by conspecifics. Batzli, Getz & Hurley (1977) did find that *M. pennsylvanicus* young were less likely to have growth suppressed by littermates than young *Microtus californicus* (Peale) and *Microtus ochrogaster* (Wagner). Facemire & Batzli (1983) suggest that growth rates in microtine rodents with a promiscuous social system that live in patchy, unpredictable environments, like *M. pennsylvanicus*, will not be suppressed by relatives.

Reproduction and age at sexual maturity

Our study shows that adults influence both the timing of the onset of sexual maturity and the proportion of young animals that become reproductive (Tables 2, 5, 6). As adult density increases, young animals, especially young females, are less likely to begin

reproduction early (Fig. 2). Again, evidence suggests that adult females are responsible for more of this suppression than adult males (Tables 2, 5).

In previous field studies, the selective removal of specific segments of microtine populations has affected reproduction in the younger cohorts, but the effects of the sexes have not been consistent. A larger proportion of young females and/or males often became reproductive, especially when individuals of the same sex had been removed (Bujalska 1973; Myllymäki 1974 (cited in Myllymäki 1977); Redfield, Taitt & Krebs 1978; Saitoh 1981; Bondrup-Nielsen 1986; Gilbert *et al.* 1986). In some manipulated populations, as in this study, females matured at weights significantly below those of females on the control grids, but males on all grids matured at approximately the same weight (Krebs, Redfield & Taitt 1978; Porter & Dueser 1986); in other studies, both sexes matured at lower weights on manipulated grids than on control grids (Boonstra 1978; Redfield, Taitt & Krebs 1978). Some of the apparent inconsistencies may be a result of differences in experimental design or individual growth rates. However, it is also likely that the pattern of suppression varies with the social system of the species (Facemire & Batzli 1983) and/or with variation in the dynamics of different regional populations (Bondrup-Nielsen & Ims 1986).

Therefore under certain social conditions most young delay reaching maturity. Why do they delay this crucial activity? Either (i) they are inhibited directly or indirectly by adult conspecifics, or (ii) the young animals delay their own reproduction.

Adult rodents can directly regulate reproductive activity in young animals. *M. musculus* adults use pheromones to accelerate or inhibit the maturation of young conspecifics as population densities change (Vandenbergh 1987). There is some evidence for these types of pheromones in *M. pennsylvanicus* (Baddaloo & Clulow 1981). Pregnancy failure resulting from male-induced blockage appears to increase in *M. pennsylvanicus* with population density and newly mature females are probably more susceptible to this pheromone than females which have already produced litters (Mallory & Clulow 1977). Therefore, adults have mechanisms to influence the timing of reproduction in young animals and these mechanisms are adjusted as population densities change.

Adults may indirectly influence young animals by forcing them into situations where they will be unable to become reproductive. As population densities increase, adults may restrict many immature animals to pockets of unsuitable habitat (Saitoh 1981), where reproduction could be suppressed by the presence of siblings (Batzli, Getz & Hurley 1977), or females may form extended families that include young from several litters, the oldest of which do not mature as long as they remain with the mother (Jannett 1978; Madison 1980; Bondrup-Nielsen & Ims 1986).

Adults may also indirectly limit reproduction in young animals by restricting their access to resources. Food availability and quality can influence reproduction (Lloyd 1970), but the addition of food to natural populations has only had limited success in increasing reproductive rates (Krebs & Delong 1965; Watts 1970b; Flowerdew 1973; Taitt *et al.* 1981). However, specific components of the vegetation that are not added in regular feeding experiments, such as the compound in green, growing plant parts that triggers the onset of breeding (Berger *et al.* 1981) and elicits sexual maturation (Negus & Pinter 1966), may not be available in sufficient quantities to young animals at higher population densities.

It has also been argued that young animals delay their own sexual maturation (Christian 1971). Males may be unable to attract a mate until they have reached some minimum size. This may explain the similar weights at maturity for young males on all of

our grids (Table 6). As subadults reach puberty, they are more likely to be wounded or killed (Rose 1979; Gipps 1983) or to be forced to leave their home territory (Howard 1960; Christian 1970; Myers & Krebs 1971; Beacham 1981; Nadeau, Lombardi & Tamarin 1981). Since a dispersing subadult's chance of surviving and reproducing may be low, it may be advantageous to delay maturation until the density of reproductive animals is lower, or until the individual has attained a greater size and can withstand older animals' aggressive pressures upon it to disperse (Christian 1971). If they do mature early and are allowed to remain, they may not be able to defend their young (Clutton-Brock & Albon 1985), or their young may be forced to disperse (Hansen & Nixon 1985). Therefore, it can be to a young animal's advantage to delay reproduction until social conditions or their own physical condition improve.

We have looked at the average response of young animals to adult density. Future research should follow individuals over their life-times and determine their total fitnesses. How long-lasting and detrimental are the effects of suppression? How much variation is there among individuals? Do adults suppress reproduction and survival in their own young or only in unrelated young?

In conclusion, *M. pennsylvanicus* adults can depress young animals' survival rates and inhibit their reproductive rates. By controlling these parameters, adults can directly reduce the number of competitors; they can also regulate two of the most important determinants of the rate of population growth (Cole 1954; Krebs 1966; Drickamer 1980). Indeed, the rate of population growth was increased by removing adults on at least two of the experimental grids, in both trials, in our study (Rodd 1982). Although the average projected fitness for a young animal is low, if conditions improve, it can become reproductive almost immediately (Bondrup-Nielsen 1986). This type of strategy, where a potential for rapid increase is closely controlled, would be useful both from the adults' and the young animals' points of view in the unpredictable, hazardous environment that they inhabit.

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REFERENCES

- Anderson, J. L. (1975). *Phenotypic correlations among relatives and variability in reproductive performance in populations of the vole* *Microtus townsendii*. Unpublished Ph.D. thesis, University of British Columbia, Vancouver, Canada.
- Baddaloo, E. G. Y. & Clulow, F. V. (1981). Effects of the male on growth, sexual maturation, and ovulation of young female meadow voles, *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **59**, 415-421.
- Batzli, G. O., Getz, L. L. & Hurley, S. S. (1977). Suppression of growth and reproduction of microtine rodents by social factors. *Journal of Mammalogy*, **58**, 583-591.
- Beacham, T. D. (1979a). Survival in fluctuating populations of the vole *Microtus townsendii*. *Canadian Journal of Zoology*, **57**, 2375-2384.

- Beacham, T. D. (1979b). Size and growth characteristics of dispersing voles, *Microtus townsendii*. *Oecologia*, **42**, 1–10.
- Beacham, T. D. (1980). Demography of declining populations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, **49**, 453–464.
- Beacham, T. D. (1981). Some demographic aspects of dispersers in fluctuating populations of the vole *Microtus townsendii*. *Oikos*, **36**, 273–280.
- Berger, P. J., Negus, N. C., Sanders, E. H. & Gardner, P. D. (1981). Chemical triggering of reproduction in *Microtus montanus*. *Science*, **214**, 69–70.
- Bondrup-Nielsen, S. (1986). Investigation of spacing behaviour of *Clethrionomys gapperi* by experimentation. *Journal of Animal Ecology*, **55**, 269–279.
- Bondrup-Nielsen, S. & Ims, R. A. (1986). Comparison of maturation of female *Clethrionomys glareolus* from cyclic and noncyclic populations. *Canadian Journal of Zoology*, **64**, 2099–2102.
- 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**, 242–248.
- Boonstra, R. (1984). Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young. *Oecologia*, **62**, 126–131.
- Boonstra, R. (1985). Demography of *Microtus pennsylvanicus* in Southern Ontario: enumeration versus Jolly–Seber estimation compared. *Canadian Journal of Zoology*, **63**, 1174–1180.
- Boonstra, R. & Krebs, C. J. (1978). Pitfall trapping of *Microtus townsendii*. *Journal of Mammalogy*, **59**, 136–148.
- Boonstra, R. & Rodd, F. H. (1983). Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology*, **52**, 757–780.
- Boonstra, R. & Rodd, F. H. (1984). Efficiency of pitfalls versus live traps in enumeration of populations of *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **62**, 758–765.
- Boutin, S. A. (1984). The effect of conspecifics on juvenile survival and recruitment of snowshoe hares. *Journal of Animal Ecology*, **53**, 623–637.
- Bujalska, G. (1973). The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility, Supplement*, **19**, 465–474.
- Christian, J. J. (1970). Social subordination, population density and mammalian evolution. *Science*, **168**, 84–90.
- Christian, J. J. (1971). Fighting, maturity and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **52**, 556–567.
- Clutton-Brock, T. H. & Albon, S. D. (1985). Competition and population regulation in social mammals. *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 557–576. Blackwell Scientific Publications, Oxford.
- Cole, L. C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology*, **29**, 103–137.
- Drickamer, L. C. (1980). Social cues and reproduction: rodents and primates. *Biosocial Mechanisms of Population Regulation* (Ed. by M. N. Cohen, R. S. Malpass & H. G. Klein) pp. 37–53. Yale University Press, New Haven.
- Dunbar, R. I. M. (1985). Population consequences of social structure. *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith) pp. 507–520. Blackwell Scientific Publications, Oxford.
- Ebling, F. J. & Stoddart, D. M. (Eds) (1978). *Population Control by Social Behaviour*. Praeger Publications, New York.
- Facemire, C. F. & Batzli, G. O. (1983). Suppression of growth and reproduction by social factors in microtine rodents: tests of two hypotheses. *Journal of Mammalogy*, **64**, 152–156.
- Flowerdew, J. R. (1973). The effect of natural and artificial changes in food supply on breeding in woodland mice and voles. *Journal of Reproduction and Fertility, Supplement*, **19**, 259–269.
- Frank, F. (1957). The causality of microtine cycles in Germany. *Journal of Wildlife Management*, **21**, 113–121.
- Gaines, M. S. & Rose, R. K. (1976). Population dynamics of *Microtus ochrogaster* in eastern Kansas. *Ecology*, **57**, 1145–1161.
- Getz, L. L., Verner, L., Cole, F. R., Hofmann, J. E. & Avalos, D. E. (1979). Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus*. *Acta Theriologica*, **24**, 319–349.
- Gilbert, B. S., Krebs, C. J., Talarico, D. & Cichowski, D. B. (1986). Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology*, **55**, 543–552.
- Gipps, J. H. W. (1983). Maturity, castration and behaviour of male bank voles, *Clethrionomys glareolus* (Mammalia). *Journal of Zoology (London)*, **200**, 197–203.
- Haigh, G. R. (1987). Reproductive inhibition of female *Peromyscus leucopus*: female competition and behavioural regulation. *American Zoologist*, **27**, 867–878.
- 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 deer mice. *Ecology*, **48**, 377–392.

- Howards, W. E. (1960). Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist*, **63**, 152–161.
- Iverson, S. L. & Turner, B. N. (1969). Under-snow shelter for small mammal trapping. *Journal of Wildlife Management*, **33**, 722–723.
- Jannett, F. J. Jr (1978). The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. *Behavioral Ecology and Sociobiology*, **3**, 245–263.
- Jolly, G. M. & Dickson, J. M. (1983). The problem of unequal catchability in mark-recapture estimation of small mammal populations. *Canadian Journal of Zoology*, **61**, 922–927.
- Keller, B. L. (1985). Reproductive Patterns. *Biology of New World Microtus* (Ed. by R. H. Tamarin) pp. 725–778. American Society of Mammalogists, Special Publication 8.
- Kikkawa, J. (1964). Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *Journal of Animal Ecology*, **33**, 259–299.
- Koshkina, T. V. & Korotkov, Y. S. (1975). Regulative adaptations in populations of the red vole (*Clethrionomys rutilus*) under optimum conditions of its range. *Fauna and Ecology of Rodents*, **12**, 5–61. (Translated by W. A. Fuller, University of Alberta.)
- Krebs, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs*, **36**, 239–273.
- Krebs, C. J. (1971). Genetic and behavioral studies on fluctuating vole populations. *Dynamics of Populations* (Ed. by P. J. Den Boer & G. R. Gradwell), pp. 243–256. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, Netherlands.
- Krebs, C. J. & Boonstra, R. (1984). Trappability estimates for mark-recapture data. *Canadian Journal of Zoology*, **62**, 2440–2444.
- Krebs, C. J. & Delong, K. T. (1965). A *Microtus* population with supplemental food. *Journal of Mammalogy*, **46**, 566–573.
- Krebs, C. J., Keller, B. L. & Tamarin, R. H. (1969). *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, **50**, 587–607.
- Krebs, C. J. & Myers, J. H. (1974). Population cycles in small mammals. *Advances in Ecological Research*, **8**, 267–399.
- Krebs, C. J., Redfield, J. A. & Taitt, M. J. (1978). A pulsed-removal experiment on the vole *Microtus townsendii*. *Canadian Journal of Zoology*, **56**, 2253–2262.
- Krebs, C. J., Wingate, I., LeDuc, J., Redfield, J. A., Taitt, M. & Hilborn, R. (1976). *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology*, **54**, 79–95.
- Leslie, P. H., Perry, J. S. & Watson, J. S. (1945). The determination of the median body-weight at which female rats reach maturity. *Proceedings of the Zoological Society of London*, **115**, 473–488.
- Lewontin, R. C. (1965). Selection for colonizing ability. *The Genetics of Colonizing Species* (Ed. by H. G. Baker & G. L. Stebbins), pp. 77–94. Academic Press, New York.
- Lloyd, H. G. (1970). Variation and adaptation in reproductive performance. *Symposia of the Zoological Society of London*, **26**, 165–188.
- Madison, D. M. (1980). Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology*, **7**, 65–71.
- Mallory, F. F. & Clulow, F. V. (1977). Evidence of pregnancy failure in the wild meadow vole, *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **55**, 1–17.
- Myers, J. H. & Krebs, C. J. (1971). Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs*, **41**, 53–78.
- Myllymäki, A. (1977). Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. *Oikos*, **29**, 553–569.
- Nadeau, J. H., Lombardi, R. T. & Tamarin, R. H. (1981). Population structure and dispersal of *Peromyscus leucopus* on Muskeget Island. *Canadian Journal of Zoology*, **59**, 793–799.
- Negus, N. C. & Pinter, A. J. (1966). Reproductive responses of *Microtus montanus* to plants and plant extracts in the diet. *Journal of Mammalogy*, **47**, 596–601.
- Neter, J., Wasserman, W. & Kutner, M. H. (1985). *Applied Linear Statistical Models*. R. D. Irwin, Inc, N.Y. U.S.A.
- Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. (1975). *Statistical Package for the Social Sciences*, 2nd edn. McGraw Hill, Inc., N.Y. U.S.A.
- Porter, J. H. & Dueser, R. D. (1986). A test for suppression of body growth and sexual maturity in small meadow voles (*Microtus pennsylvanicus*) in field enclosures. *American Midland Naturalist*, **115**, 181–190.
- Redfield, J. A., Taitt, M. J. & Krebs, C. J. (1978). Experimental alteration of sex ratios in populations of *Microtus townsendii*, a field vole. *Canadian Journal of Zoology*, **56**, 17–27.
- Rodd, F. H. (1982). *A selective removal experiment on the meadow vole, Microtus pennsylvanicus*. Unpublished M.Sc. thesis, University of Toronto, Toronto, Canada.
- Rodd, F. H. & Boonstra, R. (1984). The spring decline in the meadow vole, *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **62**, 1464–1473.
- Rose, R. K. (1979). Levels of wounding in the meadow vole, *Microtus pennsylvanicus*. *Journal of Mammalogy*, **60**, 37–45.

- Sadleir, R. M. F. S. (1965). The relationship between agonistic behaviour and population changes in the deer mouse, *Peromyscus maniculatus* (Wagner). *Journal of Animal Ecology*, **34**, 331–352.
- Saitoh, T. (1981). Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology*, **50**, 79–87.
- SAS Institute Inc. (1985). *SAS User's Guide: Statistics*, Version 5 Edition. SAS Institute Inc., Cary, N.C., U.S.A.
- Sibly, R. M. & Smith, R. H. (Eds) (1985). *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour*. Blackwell Scientific Publications, Oxford.
- Slade, N. A. & Balph, D. F. (1974). Population ecology of Uinta ground squirrels. *Ecology*, **55**, 989–1003.
- Smyth, M. (1968). The effects of the removal of individuals from a population of bank voles *Clethrionomys glareolus*. *Journal of Animal Ecology*, **37**, 167–183.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. W. H. Freeman and Company, San Francisco, U.S.A.
- SPSS Inc. (1983). *SPSS User's Guide*. McGraw Hill Book Company, New York, U.S.A.
- Summerlin, C. T. & Wolfe, J. L. (1973). Social influences on trap response of the cotton rat, *Sigmodon hispidus*. *Ecology*, **54**, 1156–1159.
- Taitt, M. J., Gipps, J. H. W., Krebs, C. J. & Dondjerski, Z. (1981). The effect of extra food and cover on declining populations of *Microtus townsendii*. *Canadian Journal of Zoology*, **59**, 1593–1599.
- Tamarin, R. H. (1977). Dispersal in island and mainland voles. *Ecology*, **58**, 1044–1054.
- Tamarin, R. H. (1980). Dispersal and population regulation in rodents. *Biosocial Mechanisms of Population Regulation* (Ed. by M. N. Cohen, R. S. Malpass & H. G. Klein), pp. 117–133. Yale University Press, New Haven, U.S.A.
- Terman, C. R. (1965). A study of population growth and control exhibited in the laboratory by prairie deer mice. *Ecology*, **46**, 890–895.
- Turner, B. N. & Iverson, S. L. (1973). The annual cycle of aggression in male *Microtus pennsylvanicus* and its relation to population parameters. *Ecology*, **54**, 967–981.
- Vandenbergh, J. G. (1987). Regulation of puberty and its consequences on population dynamics of mice. *American Zoologist*, **27**, 891–898.
- Watson, A. (1985). Social class, socially-induced loss, recruitment and breeding of red grouse. *Oecologia*, **67**, 493–498.
- Watts, C. H. S. (1970a). A field experiment on intraspecific interactions in the red-backed vole, *Clethrionomys gapperi*. *Journal of Mammalogy*, **51**, 341–347.
- Watts, C. H. S. (1970b). Effect of supplementary food on breeding in woodland rodents. *Journal of Mammalogy*, **51**, 169–171.

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