



## Regulation of Breeding Density in *Microtus pennsylvanicus*

Rudy Boonstra; F. Helen Rodd

*Journal of Animal Ecology*, Volume 52, Issue 3 (Oct., 1983), 757-780.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28198310%2952%3A3%3C757%3AROBDIM%3E2.0.CO%3B2-8>

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*Journal of Animal Ecology* is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

---

*Journal of Animal Ecology*  
©1983 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2003 JSTOR

## REGULATION OF BREEDING DENSITY IN *MICROTUS PENNSYLVANICUS*

BY RUDY BOONSTRA AND F. HELEN RODD

*Division of Life Sciences, Scarborough College, University of Toronto, West Hill,  
Ontario, Canada M1C 1A4*

### SUMMARY

(1) This study tests the hypothesis that breeding density in polygamous microtines is determined by breeding females, which compete for space to rear young. Males compete for access to females directly, not for access initially to territories.

(2) To test these predictions, we live-trapped three populations from 1978 to 1981: a Control grid; a Female grid, from which all breeding males were continuously removed; and a Male grid, from which all breeding females were continuously removed.

(3) In every spring, the number of breeding males on the Male grid declined for approximately 2 months after the onset of the breeding season, the number on the Female grid increased markedly through immigration, and the number on the Control grid remained constant or increased slightly. The number of breeding females remained constant or increased slightly on the Control and Female grids, while the number on the Male grid increased markedly through immigration.

(4) Adult males on the Control grid always had higher survival rates and longer expectations of life than did those on the Male grid throughout the breeding season. Adult females on the Control and Female grids had similar survival rates and expectations of life. Adult male survival was strongly related to the density of breeding females. Adult female survival was not related to the density of either sex.

(5) Resident breeding males restricted recruitment of other breeding males in the presence of breeding female residents, but in their absence, resident males only partially restricted other breeding males. Resident breeding females restricted recruitment of other breeding females independently of male presence.

(6) These results support the hypothesis that breeding female microtines regulate breeding density. We propose that males form dominance hierarchies to gain access to females.

### INTRODUCTION

The role of social behaviour in the regulation of animal populations is increasingly accepted (Watson & Moss 1970; Ebling & Stoddart 1978; Cohen, Malpass & Klein 1980). The social organization of animals varies enormously and, in turn, so do the mechanisms responsible for setting breeding density (Crook, Ellis & Goss-Custard 1976; Emlen & Oring 1977). In birds, at least 90% of the species studied are monogamous (Lack 1968) and a typical pattern is one in which males compete for territories and females then pair with the territory holders (Watson & Jenkins 1968; Krebs 1971). Thus males set breeding density. In mammals, less than 3% of the species are reported to be monogamous (Eisenberg 1966; Kleiman 1977) and there is no typical pattern with respect to social

organization. The breeding density in mammals may be set by males, by females, by both, or it may be sex-specific, so that males and females set their breeding density independent of that of the opposite sex.

In microtine rodents, there is increasing evidence that females set breeding density (Bujalska 1970, 1973; Boonstra 1977; Viitala 1977; Redfield, Taitt & Krebs 1978a; Madison 1980). Few studies have attempted to manipulate social structure to examine how breeding density is determined. Redfield, Taitt & Krebs (1978a, b) performed the first sex ratio manipulations in microtines to examine social structure. They (1978a) hypothesized that spacing behaviour in species such as *Microtus townsendii* (Bachman) was sex-specific. Removal of one sex was predicted to result in replacement primarily by individuals of the same sex as was removed but should not affect the density of the abundant sex. Hence, breeding density of one sex was set independently of the other. They made no predictions about the survival of the animals in the manipulated populations although, if density of the abundant sex did not change, one could expect that survival would not be affected either. From a different experimental design using the same species which involved overall density reductions in both sexes, Boonstra (1977) proposed a hypothesis in which females compete for space to promote growth and survival of young, while males compete for access to breeding females. The predictions were that if females set breeding density, removal of breeding males should have no effect on female density or survival (i.e. residency in the area). However, removal of breeding females should result in reduced male density and survival in the area. Thus, male spacing behaviour was proposed to be conditional on female presence. No direct predictions were made with respect to recruitment, though the logical consequences of this hypothesis are identical to those predicted by Redfield, Taitt & Krebs (1978a) for the population with the rare sex. In an experimental population consisting primarily of males, one would predict spacing behaviour to be less severe, since the objects of male competition would be absent. These two views of microtine social structure are not totally incompatible however, essentially differing only in the anticipated response of males to reduced female density. This experiment was designed to test the predictions made by Boonstra (1977) on *M. pennsylvanicus* (Ord).

## STUDY AREA

The study was carried out on a 10-ha grassland adjacent to the Toronto International Airport, Malton, Ontario (Fig. 1). It was completely surrounded by roads, although there were culverts connecting the area to other fields. We do not believe that the roads created an area which was effectively an island from which voles would not move, for we have seen voles cross the roads. The evidence of Getz, Cole & Gates (1978) also indicates free movement along major highways and suggests that voles move readily over side roads leading to them. A fence surrounded the entire area but did not prevent movement by small mammals. In addition to the meadow vole, *M. pennsylvanicus*, the other small mammals that occurred on the area in order of decreasing abundance were: *Peromyscus maniculatus bairdii* (Hoy & Kennicott), *Mus musculus* L., *Sorex cinereus* Kerr, and *Zapus hudsonius* (Zimmerman). The vegetation consisted predominantly of various species of grasses (*Poa pratensis* L., *Poa compressa* L., *Festuca pratensis* Huds., and *Agropyron repens* (L.) Beauv.), though various species of herbs were also common (*Solidago* spp., *Aster* spp., *Asclepias syriaca* L., *Melilotus officinalis* (L.) Lam., *Geum macrophyllum* Willd., and *Bidens frondosa* L.).

Mammalian predators occurred on the area, primarily in the spring, summer and

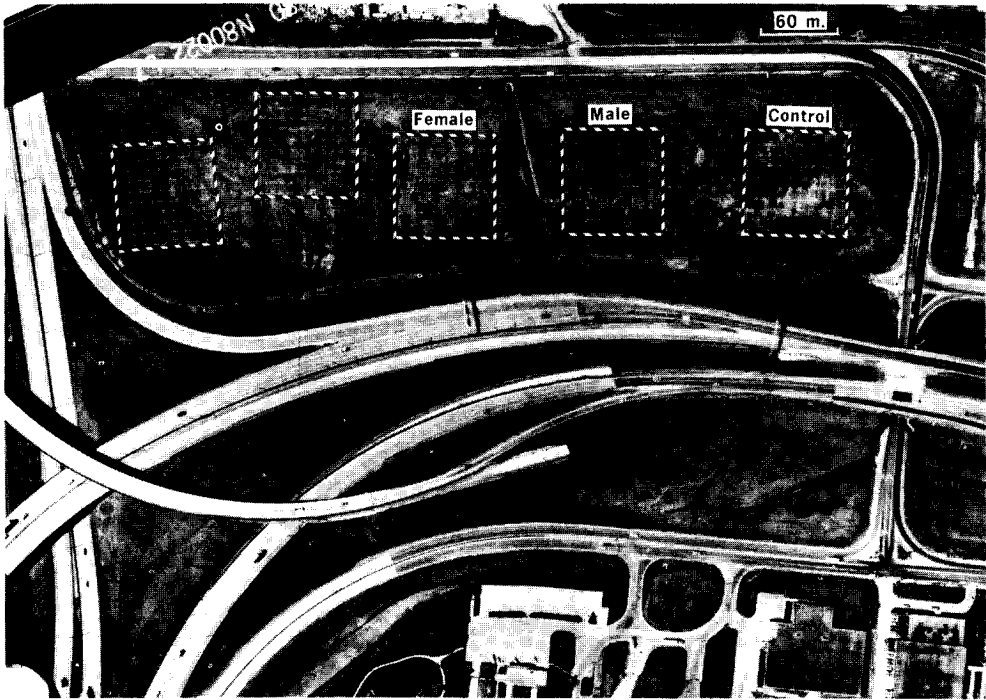


FIG. 1. Photograph of the study area near Toronto International Airport, Ontario.

autumn, and avian predators in autumn and winter. Raccoons (*Procyon lotor* L.) and skunks (*Mephites mephites* Schreber) were the most common mammalian predators. We attempted to remove all raccoons with large live-traps because they disturbed the small mammal traps. Skunks, if caught, were simply released. Only one weasel (*Mustela erminea* L.) was seen on the area, in June 1981, and no faeces were found at any other time. Rats (*Rattus norvegicus* Berkenhout) killed some voles, especially in the winter of 1979–80, but these rats were removed. The most common avian predators were rough-legged hawks (*Buteo lagopus* Pontoppidan), kestrels (*Falco sparverius* L.), and red-tailed hawks (*Buteo jamaicensis* Gmelin). A snowy owl (*Nyctea scandiaca* L.) was seen once.

## METHODS

On 26 June 1978, three trapping grids were set up (Fig. 1): a Control grid, which was simply live-trapped; a Male grid, from which all breeding females were continuously removed; and a Female grid, from which all breeding males were continuously removed. Each grid was separated from the next by at least 60 m. Two other grids involved in a different experiment (Rodd 1982), were trapped during the autumn, winter, and spring of 1978–79 and 1979–80. The Female grid was separated from the first of these by 30 m. Each 0.7-ha grid had 100 trapping points arranged in a 10 × 10 pattern at 7.6-m intervals. Longworth live-traps were placed at every station and baited with oats; cotton bedding was provided for warmth. Except for the first trapping session, the Control grid always had at least 150 traps and up to 200 during periods of high vole density. The Female and Male grids had from 100 to 150 traps. The Control grid was simultaneously trapped with

pitfall traps (Boonstra & Krebs 1978), but few of those data will be reported here. The animals caught in pitfalls were predominantly the young which were not as readily caught in live-traps. Thus, the data collected on the Control and the two experimental grids were comparable. In the autumn of 1978, all traps on the Control grid were covered with snow covers (Iverson & Turner 1969), to permit trapping in the winter. Trap stations on the Female and Male grids were supplied with these snow tunnels in the spring of 1980.

Traps were set every second week in the afternoon, checked the following morning, the next afternoon, and again on the second morning, when they were locked open and left in place. During the summer, traps were set only in the evenings to avoid mortality in traps during the heat of the day. The Control grid was trapped regularly throughout the study, except in the winter of 1980–81, when a 4-week trapping interval was used. The Female and Male grids were trapped from 2 July to 22 November 1978, from 29 March to 23 November 1979, from 26 March to 21 November 1980, and from 11 March to 17 July 1981.

All voles were ear-tagged, and on each capture the following data were recorded: tag number, trap location, body weight, wounding on the lower back and rump, sex, and sexual condition. Sexual condition in males was determined by testes position (scrotal or abdominal); in females by the presence of lactating tissue (present or absent based on nipple size and appearance), vaginal perforation, separation of the pubic symphysis (closed, slightly open, or open), and obvious pregnancy. In this study, voles were classified as adult (>33 g), sub-adult (22–33 g), or juvenile (<22 g). This classification was the result of an analysis of the median weight at sexual maturity (Leslie, Perry & Watson 1945) based on pooled data from the spring and summer breeding seasons from the Control grid and from a similar grid 30 km north of Toronto. This weight classification was similar to that used by Krebs, Keller & Tamarin (1969).

Population variables were determined by enumeration (Krebs 1966). This method requires that a large proportion of the individuals of trappable age be captured every session. A minimum trappability estimate was calculated by the formula given in Boonstra & Krebs (1978). The data from our study were divided into a spring breeding period (April–June), a summer breeding period (July–August), and an autumn–winter period (September–March) during which breeding was absent or of low intensity. During the spring, the minimum trappability on the Control grid averaged 70% for the males and 76% for the females, while on the experimental grids it was 6–7% higher. During summer, the minimum trappability on the Control averaged 52% for the males and 60% for females, while that on the experimental grids was 3–5% higher. In winter, the minimum trappability on the Control averaged 61% for males and 66% for females while the trappabilities were similar or slightly lower on the experimental grids. These winter trappabilities were lower than reported in other studies because severe winter weather often restricted trapping to one day only and because densities were generally very high.

## RESULTS

### *Population density*

We asked two questions with respect to population density: first, what was the impact of the manipulations on the total population density on each grid; and second, how did the populations of breeding animals respond to the manipulations? Since it is the breeding animals which are responsible for most of the changes in the demography of the population, we expected that it would be this group which would respond immediately.

Males were in breeding condition if they were scrotal, and females were in breeding condition if they were perforate, lactating, or pregnant.

### Total population density

Five main points are shown in Fig. 2. (i) The population density on the Control grid was generally high throughout this study, ranging from a low of 67 in the spring of 1979 to a high of 384 in the autumn of 1980. (ii) The initial populations on the Female and Male grids were similar to that on the Control (note that cropping did not start until the second trapping session). Hence, we believe that the areas were similar in their capacity to support equal numbers of animals. (iii) The overall effect of the manipulations on the Male and Female grids was to create populations which were generally one-half to two-thirds as numerous as that on the Control. However, there were periods of recruitment of young, nonbreeding animals when the densities on one or both the experimental grids approached that on the Control grid (August–September 1978, July–October 1979, and June 1981). (iv) Declines occurred on the control grid in every year, but only in 1980 was the decline restricted to the spring, whereas in 1979 and 1981 the decline started in the winter and continued into the spring. The decline in 1979 was peculiar because a portion of it could be explained by severe winter weather, while that of 1980 could not. It also resulted in the lowest density year seen. In December 1978 and again in January 1979, periods of freezing rain occurred (2.3 and 1.8 cm, respectively) followed by prolonged periods of intense cold (down to  $-19^{\circ}\text{C}$  for 24 days), resulting in numerous cases of presumed starvation and cannibalism. In March and April, when weather conditions had improved markedly, the population on the Control continued to decline because of dispersal (see dispersal section). A similar decline must also have occurred on the Female and Male grids. The spring declines which occurred on these grids in all years were in part a

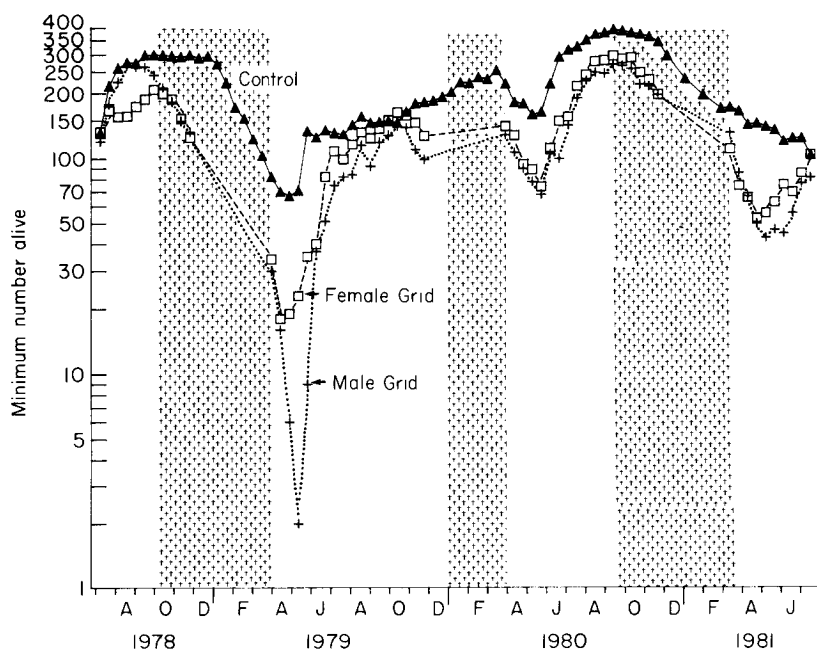


FIG. 2. Minimum number of *M. pennsylvanicus* on the three live-trapping grids. Nonbreeding periods are shaded.

reflection of the cropping procedure. However, they were also a real phenomenon, primarily on the Male grid, reflecting poor survival and dispersal of the residents.

### Breeding population density

*Males.* On the Control grid 1979 stood out as the only year in which the number of breeding males actually increased as the breeding season progressed (Fig. 3). This was largely the result of recruitment of maturing young of the year. Even then, the number of breeding males did not exceed thirty-six animals. In both 1980 and 1981, the maximum number of breeding males (seventy-three and eighty, respectively, which were almost double that found on the grid in 1979) was reached at the onset of breeding in the spring, and this number was not exceeded as the breeding season progressed.

On the Female grid, the initial number of breeding males in each spring was ten to fifteen animals lower than on the Control grid. The males removed in the first 2 months of the spring were all overwintered animals. To obtain an index of the different rates of recruitment and movement onto the Female grid in different years, we calculated the recovery ratio index (Krebs *et al.* 1976) (ratio of the number of breeding males removed from the Female grid divided by the average male density on the Control grid). The index was calculated for the 1-month period (three trapping sessions) after the overwintering residents had been removed from the Female grid. The indices for 1979, 1980, and 1981 were 0.12, 0.35, and 0.29. Thus, in 1979 few males moved onto the Female grid to replace the original overwintering residents, indicating that there were few potential immigrants. However, in both 1980 and 1981, relatively large numbers of overwintered males moved onto the area (Fig. 3). After this period, young males born on the area and elsewhere were maturing, so that the number of breeding males removed from the Female grid then

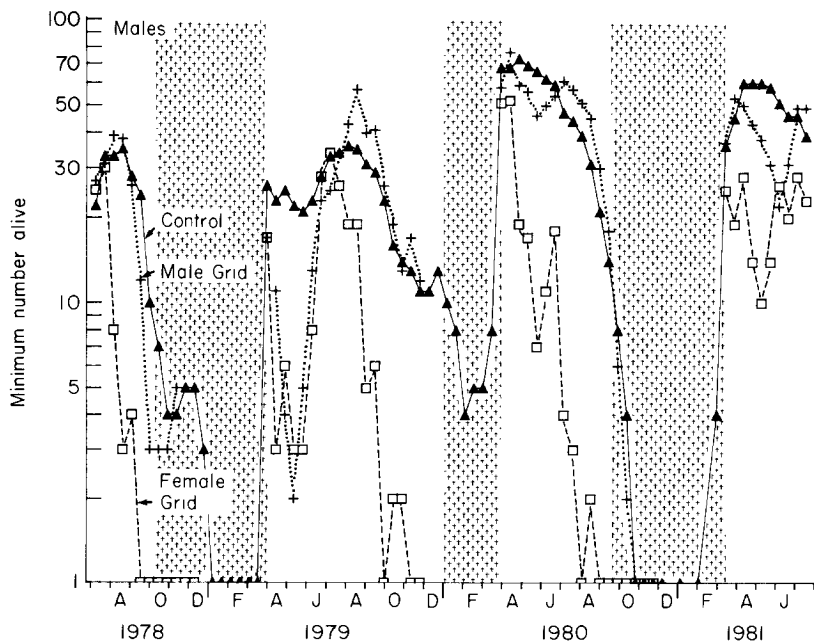


FIG. 3. Minimum number of breeding male *M. pennsylvanicus* on the three live-trapping grids. Nonbreeding periods are shaded.

represented a composite of mainly young of the year and some overwintered males. The number of breeding males entering the population generally increased for a time (late June–August 1979, July 1980, June–July 1981). Thereafter few breeding males entered the population. Only seventeen, fifteen, and eleven breeding males moved onto the Female grid in 1978, 1979, and 1980 respectively in the last 12–14 weeks of the breeding season. Thus, during the last 3 months of the breeding season, few males entered a male deficient area.

On the Male grid, the removal of females each spring resulted in an immediate decline in the numbers of males, a decline that lasted for almost 2 months (Fig. 3). Male numbers started increasing when maturing young of the year started entering the population. Thereafter, the number of breeding males increased rapidly and actually exceeded the number present on the Control grid for a period of up to 2 months. There were more breeding males on the Male grid in 1979 from 1 August to 12 October (ranging from three to twenty-two males), in 1980 from 2 July to 10 September (ranging from four to fourteen males, and in 1981 from 1 July to 15 July (the termination of the study—ranging from three to ten males).

*Females.* As with the breeding males, 1979 was the only year in which the number of breeding females increased substantially on the Control grid (Fig. 4). In neither 1980 nor 1981 was the maximum number of breeding females in the spring exceeded as the season progressed. The maximum number of breeding females was similar in 1978 (though the spring was not trapped), 1979, and 1981 (fifty-nine, sixty-seven and sixty-one, respectively), but was considerably higher in 1980 (eighty-five).

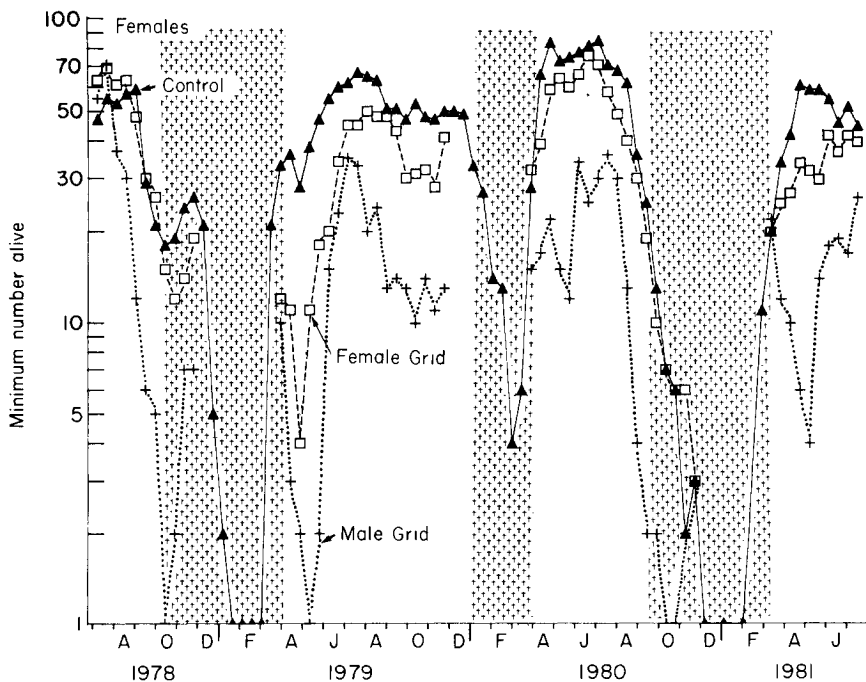


FIG. 4. Minimum number of breeding female *M. pennsylvanicus* on the three live-trapping grids. Nonbreeding periods are shaded.



On the Female grid, removal of breeding males resulted in no marked decline of breeding females in any spring (Fig. 4). A decline in numbers in April 1979 did apparently occur but was simply because some females had temporarily become imperforate. No real decline had occurred because the females had perfect survival during the 2-week interval. In each breeding season, fewer breeding females were initially found on the Female grid than on the Control, but as the season progressed, the numbers of breeding females increased every year, unlike numbers on the Control grid.

On the Male grid, the number of females removed in each spring progressively declined for 2 months prior to recruitment of young of the year (Fig. 4), indicating that few breeding females were immigrating onto the grid. The recovery ratio indices for breeding females for a 1-month period after the removal of overwintering residents for 1979, 1980, and 1981 were 0.01, 0.26, and 0.14. Thus, recruitment of females onto the Male grid was extremely low in 1979 relative to the other 2 years. Thereafter, a major pulse of females entered the Male grid, lasting about 5 months in 1979, 2 months in 1980, and at least 2 months in 1981. In 1979, these females were primarily young of the year, whereas in the other 2 years, they represent a composite of both overwintered females and young of the year.

We conclude that the absence of females during the onset of breeding in spring resulted in a drastic drop in male numbers from the Male grid, whereas an absence of males resulted in no drop in female numbers from the Female grid. During the main breeding season when young were maturing, large numbers of breeding males and females were recruited to the Female and Male grids respectively.

#### *Sex ratio*

For this experiment to have any effect, the sex ratio had to be drastically altered from that on the Control grid. Sex ratio in microtines has often been expressed as the ratio of the total number of males to females. However, from the standpoint of understanding spacing behaviour, it is probably only those actually engaged in breeding that are crucial to the population processes. We therefore examined the impact of experimental manipulations on the sex ratio of breeding animals. Sex ratio in Fig. 5 is expressed as the percentage of males in the total breeding population.

The sex ratio on the Control grid usually favoured females during the breeding season. The general pattern indicated that males were relatively more numerous at the start of the breeding season than later on. Throughout the summer of 1978, most of the breeding season of 1979, and the summer portion of 1980, between 30 and 40% of the breeding population were males. In contrast, in 1981, the breeding population on the Control consisted of about 50% males until July. On the Female grid, the continuous removal of breeding males created a population that generally consisted of less than 40% males and this was almost always below the percentage found on the Control grid. During the spring reorganization and the early portion of the main breeding season, when large numbers of breeding males recruited to the grid, the sex ratio approached that of the Control (especially in 1979). However, in the latter half of the breeding season there was usually less than 20% males in the breeding population. On the Male grid, the continuous removal of breeding females created a breeding population with usually 60–80% males. The pronounced fluctuations in this level indicated, however, that large numbers of breeding females were entering the population, primarily when young of the year were maturing elsewhere (e.g. June/July 1979, June–August 1980, and June–July 1981) (Fig. 4). Thus, our objective of a major alteration of sex ratio of breeding animals was met.

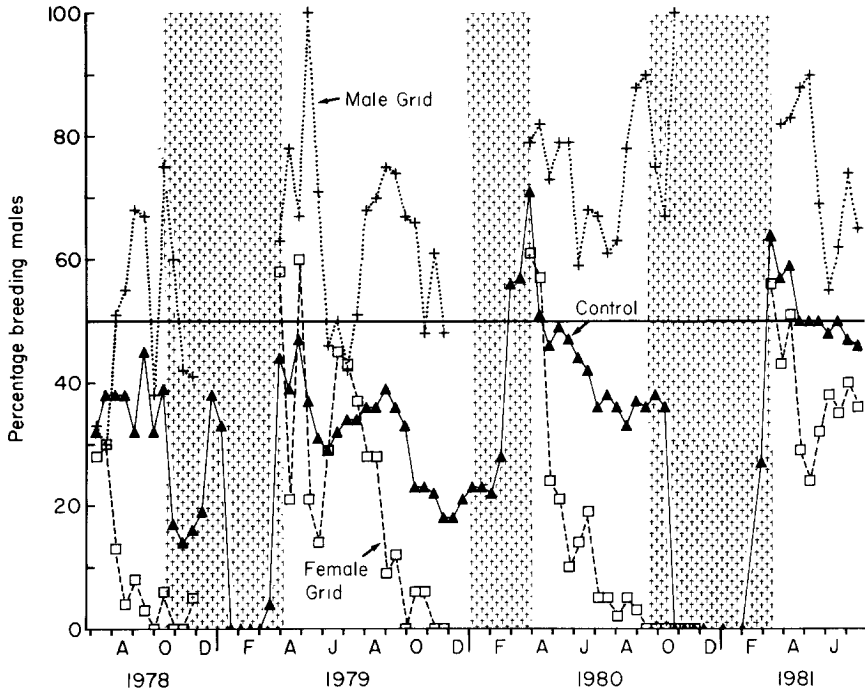


FIG. 5. Sex ratio of breeding *M. pennsylvanicus* expressed as the percentage of breeding males. Nonbreeding periods are shaded.

### Reproduction

If manipulations on the Female and Male grids influenced the reproductive status of the remaining animals, this might have affected their spacing behaviour. To assess whether any differences occurred between the Control and the experimental grids, we studied the percentage of adult males breeding and the percentage of adult females lactating. The onset of the breeding season was defined as that date when the percentage of males breeding exceeded 50%. About 4–6 weeks after this date, the percentage of females lactating generally increased rapidly. The end of the breeding season was defined as that date when less than 20% of the females were lactating.

The breeding season was longest in 1979, from the beginning of April to the end of December (Fig. 6), and this was also the year of lowest spring density. The shortest season occurred in 1980, from the beginning of April to mid-September (Figs 6, 7), and this was the year of highest spring density. Only a few bred in the winter of 1978–79, until the end of December, and in 1979–80 until February. Generally, the percentage of males breeding on the Control and Male grids was similar throughout each breeding season (Fig. 6). There were always fewer adult males in breeding condition on the Male than on the Control grid during the last 2 months of the breeding season in 1978 (Sign test: 7+, 0–,  $P < 0.01$ ), and again in 1979 from late August to mid-November (7+, 0–,  $P < 0.01$ ), but not in 1980. Female breeding intensity was similar on the Control and Female grids (Fig. 7), indicating that the absence of resident males did not affect pregnancy rates. In general, we conclude that the manipulations on the experimental grids did not depress breeding intensity below that on the Control during the main breeding season.

Regulation of breeding density

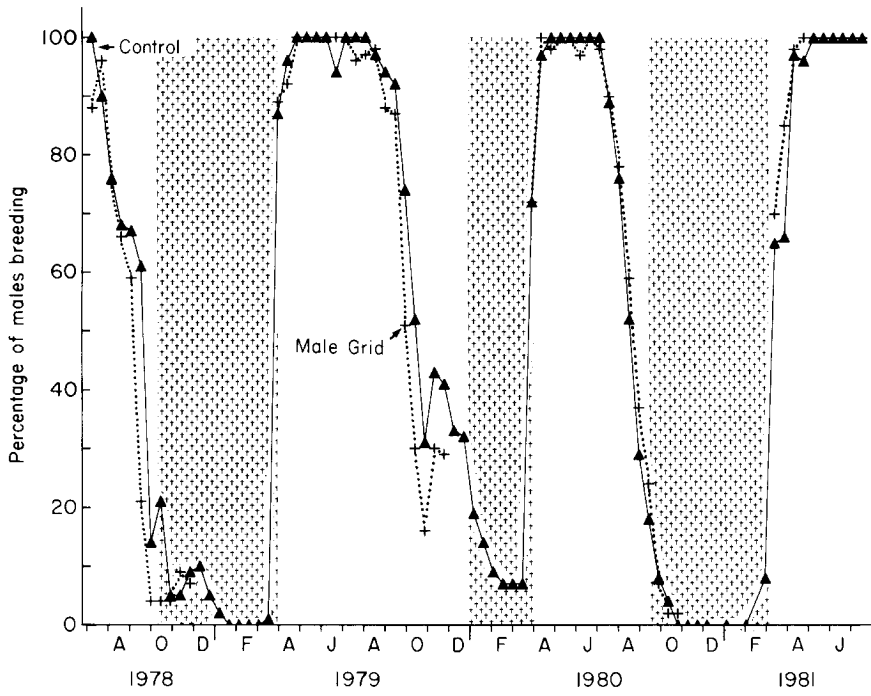


FIG. 6. Percentage of adult male *M. pennsylvanicus* in breeding condition. Nonbreeding periods are shaded.

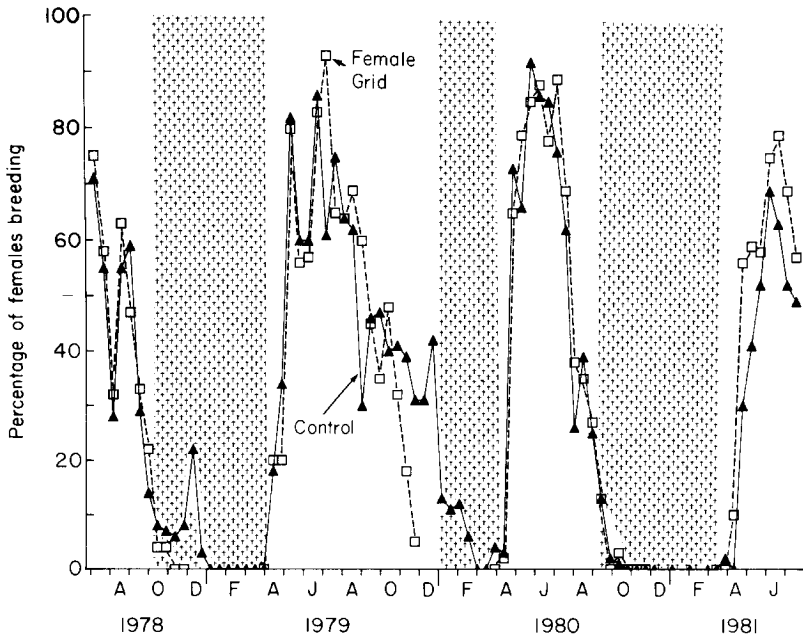


FIG. 7. Percentage of adult female *M. pennsylvanicus* in breeding condition. Nonbreeding periods are shaded.

*Survival*

We expected that animals on the Male grid would suffer the lowest survival rates relative to those on the Control grid. Minimum survival rates per 14 days of animals from one trapping session to the next were calculated. These survival rates include two components, death and emigration, which can not be separated from the trapping data available (but see dispersal section below). Nevertheless, they provide a measure of the residency on the study areas and are summarized for the spring and summer periods, when breeding was most active (Table 1). Note that survival rates are not given for adult males on the Female grid nor for adult females on the Male grid since these animals were almost always removed on first capture.

Adult males on the Control grid always survived significantly better than those on the Male grid in every spring-early summer period, when breeding was most intense (Fig. 6), the difference being largest in 1979 (20%). Adult males on the Control grid survived better in the summer period, but this was significant only in 1978 and 1980. In contrast, adult females on the Control and Female grids had very similar survival rates in both spring and summer of every year. Thus, one of the predictions of the hypothesis was fulfilled.

TABLE 1. Minimum survival rates per 14 days for *M. pennsylvanicus*. Comparisons are made between the experimental grid and the control grid within a period. Sample sizes are in parentheses

|                       | Adult       | Males<br>Sub-adult | Juvenile   | Adult      | Females<br>Sub-adult | Juvenile  |
|-----------------------|-------------|--------------------|------------|------------|----------------------|-----------|
| 1978                  |             |                    |            |            |                      |           |
| 31 July-31 August     |             |                    |            |            |                      |           |
| Control               | 0.87 (103)  | 0.86 (115)         | 0.65 (20)  | 0.94 (179) | 0.86 (70)            | 0.69 (13) |
| Female                |             | 0.77 (52)          | 0.83 (6)   | 0.91 (161) | 0.85 (48)            | 0.86 (7)  |
| Male                  | 0.73† (132) | 0.75* (170)        | 0.90 (21)  |            | 0.69* (108)          | 0.68 (19) |
| 1979                  |             |                    |            |            |                      |           |
| 25 April-20 July      |             |                    |            |            |                      |           |
| Control               | 0.88 (201)  | 0.44 (39)          | 0.51 (45)  | 0.90 (362) | 0.87 (53)            | 0.72 (50) |
| Female                |             | 0.46 (41)          | 0.69 (26)  | 0.89 (149) | 0.86 (37)            | 0.79 (29) |
| Male                  | 0.68‡ (111) | 0.42 (21)          | 0.64 (11)  |            | 1.00 (19)            | 1.00 (3)  |
| 1979                  |             |                    |            |            |                      |           |
| 1 August-14 September |             |                    |            |            |                      |           |
| Control               | 0.86 (96)   | 0.83 (30)          | 0.65 (17)  | 0.89 (214) | 0.67 (18)            | 0.78 (9)  |
| Female                |             | 0.86 (56)          | 0.78 (46)  | 0.88 (184) | 0.97* (29)           | 0.74 (38) |
| Male                  | 0.80 (152)  | 0.66 (80)          | 1.00 (1)   |            | 0.86 (28)            | 1.00 (1)  |
| 1980                  |             |                    |            |            |                      |           |
| 19 April-4 July       |             |                    |            |            |                      |           |
| Control               | 0.84 (353)  | 0.81 (84)          | 0.85 (107) | 0.92 (500) | 0.66 (94)            | 0.71 (82) |
| Female                |             | 0.77 (35)          | 0.72 (39)  | 0.91 (398) | 0.80 (44)            | 0.70 (27) |
| Male                  | 0.72‡ (359) | 0.58* (38)         | 1.00 (11)  |            | 0.82 (17)            | 1.00 (10) |
| 1980                  |             |                    |            |            |                      |           |
| 14 July-29 August     |             |                    |            |            |                      |           |
| Control               | 0.84 (175)  | 0.86 (199)         | 0.89 (28)  | 0.91 (269) | 0.93 (210)           | 0.82 (33) |
| Female                |             | 0.82 (146)         | 0.56* (41) | 0.94 (247) | 0.86 (141)           | 0.71 (63) |
| Male                  | 0.75* (234) | 0.65‡ (160)        | 0.70 (10)  |            | 0.72‡ (148)          | 0.55 (20) |
| 1981                  |             |                    |            |            |                      |           |
| 11 March-3 July       |             |                    |            |            |                      |           |
| Control               | 0.86 (393)  | 0.27 (15)          | 0.55 (11)  | 0.89 (399) | 0.83 (113)           | 0.44 (9)  |
| Female                |             | 0.63 (19)          | 0.43 (7)   | 0.86 (229) | 0.88 (74)            | 0.91 (11) |
| Male                  | 0.72‡ (292) | 0.73 (15)          |            |            | 0.50 (2)             | 1.00 (1)  |

\*  $P < 0.05$ . †  $P < 0.01$ . ‡  $P < 0.001$ .

The manipulations did not have a clear effect on the young. Sub-adult males showed no consistent differences in survival between the Control and Male grids in spring, but in summer those on the Control always survived better (significant in 1978 and 1980) than those of the Male grid. In the spring-early summer period, there were no consistent differences in survival. In sub-adult females and in juvenile males and females, there were no consistent differences in survival between the control and experimental grids.

We examined the expectation of further life for all animals alive at the start of the manipulations in each spring (Leslie *et al.* 1955). Overwintered males on the Control consistently had longer expectations of life than did those on the Male grid (significant in 1979 and 1981) (Table 2). Overwintered females on the Control and Female grids had similar expectations of life in all 3 years (Table 2). This evidence echoes the survival data presented above, indicating that females were not affected by male absence, whereas males survived poorly when females were absent.

TABLE 2. Expectation of further life in weeks ( $\pm$ S.E.) for cohorts of *M. pennsylvanicus* alive at the start of the breeding season. Sample size in parentheses

|               | Males                 |                     | Females              |                      |
|---------------|-----------------------|---------------------|----------------------|----------------------|
|               | Control grid          | Male grid           | Control grid         | Female grid          |
| 28 March 1979 | 16.8 $\pm$ 2.41 (30)  | 4.7 $\pm$ 1.64 (19) | 23.5 $\pm$ 2.69 (46) | 21.8 $\pm$ 4.84 (16) |
| 26 March 1980 | 10.7 $\pm$ 1.14 (100) | 8.5 $\pm$ 1.12 (80) | 19.8 $\pm$ 1.36 (96) | 20.7 $\pm$ 1.64 (65) |
| 11 March 1981 | 10.8 $\pm$ 0.77 (58)  | 7.2 $\pm$ 0.68 (56) | 10.7 $\pm$ 0.68 (81) | 9.6 $\pm$ 0.88 (47)  |

The nature of the manipulations allowed us to ask whether survival was related to density. We divided the breeding population into breeding residents, defined as individuals that had been on the grid for at least one complete 2-week period, and total breeding population, which included breeding residents plus newly-caught recruits in breeding condition. These latter animals would have been immediately removed if they were of the wrong sex on the experimental grids. Adult male survival was not related to the mean density of breeding male residents in either spring ( $r = 0.44$ ,  $n = 6$ ) or summer ( $r = -0.14$ ,  $n = 6$ ) but was directly related to the density of breeding resident females in both spring ( $r = 0.87$ ,  $n = 6$ ,  $P < 0.05$ ) and summer ( $r = 0.89$ ,  $n = 6$ ,  $P < 0.02$ ). In contrast, adult female survival was not related to the density of either resident breeding males (spring  $r = 0.51$ ,  $n = 6$ ; summer  $r = -0.01$ ,  $n = 6$ ) or females (summer  $r = -0.21$ ,  $n = 6$ ). There was a suggestion of a relationship between adult female survival and resident breeding female density in spring ( $r = 0.77$ ,  $n = 6$ ,  $P < 0.10$ ). However, the range in survival rates of the females was only from 0.86 to 0.94 per 2 weeks (cf. the range in males from 0.68 to 0.88, Table 1). We conclude that adult female survival showed little relationship to female density in spring. In neither sex were the correlations with mean total breeding density any different from what has already been presented and they were always lower. Thus, adult males survived better when there were more breeding females, adult females survived no better at high or low densities of breeding males, and neither sex survived better at lower densities of the same sex.

#### Dispersal

The arrangement of the grids on the study area allowed us to detect some of the losses due to emigration. We expected that many breeding males would disperse from the Male

grid while females would not disperse from the Female grid. When an animal moved from one grid to another it was assumed to have dispersed immediately after its last capture on its home grid.

Most of the dispersal from the Control grid was concentrated in the spring-early summer period but this could be separated into two reasonably distinct periods. The first period—termed the spring reorganization—occurred just prior to or at the onset of breeding in the spring and the second period—termed the main breeding season—occurred as the young of the year started to enter the population.

During the spring reorganizations of 1979 and 1980, most of the individuals leaving the Control were males (Table 3). The magnitude of the dispersal of males from the Male grid was similar to that on the Control for these 2 years, but in 1981 a marked difference occurred. While dispersal remained high from the Male grid, it dropped to very low levels from the Control grid which were significantly below that of previous years ( $P < 0.001$ ). Among females, similar low numbers dispersed from the Control and Female grids in all years (Table 3).

During the main breeding season, 1979 stood out as the year when the largest amount of dispersal between the Control and the other grids occurred (Table 3). A greater percentage

TABLE 3. Dispersal of *Microtus pennsylvanicus* from trapping grids. Percentage of the population dispersing is equal to the number of tagged animals moving to the grids divided by the total number of tagged animals on the grid  $\times 100$ . The value in parentheses indicates the number of animals present at the beginning of the period plus those entering the population during the period. Comparisons were made between the Control grid and the experimental grids within a period

|                        | Males<br>Percentage of<br>population<br>dispersing | Females<br>Percentage of<br>population<br>dispersing |
|------------------------|--|--|
| Spring reorganization  |  |  |
| 1979 1 March–27 April  |  |  |
| Control                | 37 (65)  | 6 (62)   |
| Female                 |  | 6 (17)   |
| Male                   | 45 (20)  |  |
| 1980 13 March–2 May    |  |  |
| Control                | 32 (161)   | 6 (135)  |
| Female                 |  | 8 (85)   |
| Male                   | 30 (125)   |  |
| 1981 26 February–7 May |  |  |
| Control                | 7 (108)  | 6 (115)  |
| Female                 |  | 0 (56)   |
| Male                   | 43 (87)†   |  |
| Main breeding season   |  |  |
| 1979 10 May–15 August  |  |  |
| Control                | 53 (116)   | 22 (125)   |
| Female                 |  | 14 (120)   |
| Male                   | 32 (134)*  |  |
| 1980 15 May–15 August  |  |  |
| Control                | 9 (214)  | 6 (206)  |
| Female                 |  | 7 (245)  |
| Male                   | 2 (255)*   |  |
| 1981 19 May–3 July     |  |  |
| Control                | 13 (83)  | 11 (94)  |
| Female                 |  | 7 (73)   |
| Male                   | 26 (90)†   |  |

\*  $P < 0.01$ . †  $P < 0.001$ .

of the male population dispersed from the Control grid in 1979 as compared with 1980 and 1981 ( $P < 0.001$ ) and the same relationship held for females ( $P < 0.05$ ). Generally fewer females than males dispersed, and this was most pronounced in 1979. The dispersal of animals from the Male grid differed significantly from that on the Control during the main breeding season (Table 3). In 1979 and 1980, a smaller percentage of the population dispersed from the Male grid than from the Control grid. In 1981, the reverse situation occurred. In females, there were no significant differences between the Control and Female grids.

Overall, the general pattern was one in which 1979 was a high year, 1980 a low year, and 1981 an intermediate year for dispersal from all grids. We conclude that a large percentage of the male population dispersed from the Male grid during the spring reorganization of each year irrespective of what occurred on the Control grid. During the main breeding season, there was no clear trend. In contrast, a similar low percentage of females dispersed from the Control and Female grids.

#### Recruitment

Recruitment to a population may be the result either of immigration to or birth in the area. A breeding animal that is recruited to the population is more likely to have been born elsewhere. We examined whether breeding animals restrict recruitment of other breeding animals and defined a breeding recruit as any newly-tagged vole in breeding condition above 21 g.

*Males.* During the spring-early summer period when breeding was most intense, three to four times more breeding males were recruited to the Female grid as to the Control grid (Table 4). Even on the Male grid, two to three times more breeding males were recruited as to the Control grid. During summers when density was high and breeding activity was declining (1978 and 1980), similar numbers of males were recruited to the Female and Control grids. During summers when density was low and breeding activity intense (1979) (Figs 3, 6), ten times more males were recruited to the Female grid. In all summers, there were always more breeding males being recruited to the Male grid than to the other two grids, although the difference in 1979 was only slight between the Male and Female grids.

To find out what factors were associated with the number of breeding recruits, we carried out correlation analysis between the mean number of breeding male recruits entering the population per trapping session and the mean number of resident males and females per trapping session. Resident animals were defined as those that had been trapped on the grid for at least two trapping sessions. Only the spring-early summer period was

TABLE 4 Number of breeding adults and sub-adults *Microtus pennsylvanicus* recruiting to the trapping grids

|                        | Control<br>grid | Males<br>Female<br>grid | Male<br>grid | Control<br>grid | Females<br>Female<br>grid | Male<br>grid |
|------------------------|-----------------|-------------------------|--------------|-----------------|---------------------------|--------------|
| Spring-early summer    |                 |                         |              |                 |                           |              |
| 1979 25 April-20 July  | 17              | 51                      | 48           | 11              | 31                        | 53           |
| 1980 9 April-4 July    | 29              | 108                     | 75           | 21              | 37                        | 140          |
| 1981 25 March-17 July  | 37              | 166                     | 79           | 14              | 26                        | 115          |
| Summer                 |                 |                         |              |                 |                           |              |
| 1978 August            | 10              | 10                      | 28           | 16              | 6                         | 66           |
| 1979 August            | 3               | 31                      | 32           | 7               | 10                        | 45           |
| 1980 14 July-29 August | 3               | 6                       | 17           | 1               | 17                        | 74           |

examined because breeding was most intense at that time in all 3 years. When the 1979 data were included, there was no correlation between breeding male recruits and either male residents ( $r = -0.57$ ,  $n = 9$ ) or female residents ( $r = 0.23$ ). The partial correlation coefficient between male recruits and male residents with female residents held constant ( $r_{12.3} = -0.55$ ) was not an improvement over the simple correlation. For this analysis to be instructive, there must be a potential source of recruits to enter the cropped grids. In 1979, this pool of recruits was extremely low because of the previous severe winter. For example, in the three trapping sessions after the removal of overwintered residents from the experimental grids, only three and eight males entered the Male and Female grids respectively in 1979, compared with thirty-four and seventy-two in 1980 and twenty-one and fifty-eight in 1981. It was only after the young of the year started maturing that recruitment increased. Because of the virtual absence of potential recruits in the initial portion of the breeding season in 1979, we eliminated that year from the analysis. There was now a significant negative correlation between breeding male recruits and male residents ( $r = -0.92$ ,  $n = 6$ ,  $P < 0.05$ ) but no correlation between breeding male recruits and breeding female residents ( $r = 0.24$ ). Thus, recruitment of breeding males is restricted by the presence of breeding resident males. However, since recruitment onto the Male grid was also very high (Table 4) compared with that on the Control grid, these data indicate that breeding males in the presence of breeding female residents restrict recruitment of breeding males, but in the absence of the female residents, males only partially restrict other breeding males from entering the population.

*Females.* During the spring-early summer period, recruitment of breeding females was five to eight times greater onto the Male grid than onto the Control grid (Table 4). These were not just young animals that had been born on the area but were not captured until they were in breeding condition. A large proportion of these breeding females were already adults when they arrived on the Male grid (e.g. in 1980, 110 out of 140 were adult females and in 1981, 64 of 115 were adults). Slightly more females also were recruited to the Female grid. In summer, similar low numbers of breeding females entered both the Control and Female grids, whereas large numbers continued to enter the Male grid. The recruitment of breeding females in the spring-early summer period (excluding the 1979 data) was negatively correlated with the density of breeding resident females ( $r = -0.81$ ,  $n = 6$ ,  $P < 0.05$ ), but not with the density of breeding resident males ( $r = 0.20$ ). The partial correlation between female recruits and resident density with male resident density held constant ( $r_{12.3} = -0.81$ ) was not an improvement over the simple correlation. Thus, resident breeding females restrict recruitment of other breeding females independent of male presence.

#### *Movements*

Is the use of space affected by the presence or absence of the opposite sex? We used the change in position of capture from one trapping period to the next as an index of the use of space.

Adult males on the Control grid generally had greater movements than adult females, and this was most pronounced during the spring-early summer period ( $P < 0.001$  in all 3 years) (Table 5). In summer, adult males on the Control grid moved significantly more than adult females only in August 1978 ( $P < 0.05$ ). Adult males and adult females on the Male and Female grids respectively moved more than the same sex on the Control in both the spring-early summer periods and in the late summer periods (Sign test for each of the four comparisons: 0+, 6-,  $P < 0.05$ ). In adult males, movement on the Control and Male



TABLE 5. Mean distance (m) between successive positions of capture for adult *Microtus pennsylvanicus*. Distance was measured from first capture point in trapping period  $t$  to the first capture in trapping period  $t + 1$ . Sample sizes are in parentheses. Comparisons were made within a sex within a period between the control and experimental grids

|                        | Males        |             | Females      |             |
|------------------------|--------------|-------------|--------------|-------------|
|                        | Control grid | Male grid   | Control grid | Female grid |
| 1978 August            | 7.0 (51)     | 7.6 (60)    | 4.8 (107)    | 6.1 (86)    |
| 1979 28 March–20 July  | 14.0 (164)   | 21.6‡ (65)  | 7.9 (314)    | 13.1‡ (123) |
| 1979 August            | 11.0 (63)    | 15.5† (82)  | 8.8 (139)    | 9.4 (116)   |
| 1980 26 March–4 July   | 11.3 (347)   | 12.2 (281)  | 6.4 (515)    | 7.3 (386)   |
| 1980 14 July–29 August | 6.1 (137)    | 10.4‡ (155) | 4.9 (229)    | 6.4* (206)  |
| 1981 12 March–17 July  | 11.3 (339)   | 11.9 (227)  | 5.5 (381)    | 8.5‡ (217)  |

\*  $P < 0.05$ . †  $P < 0.01$ . ‡  $P < 0.001$ .

grids was inversely correlated with the mean resident breeding male density ( $r = -0.81$ ,  $n = 6$ ,  $P < 0.05$ ) in the spring–early summer period, but not with total male density or total overall density of both sexes. Obviously, since no breeding female residents were available, it was not possible to carry out the correlation between female density and male movement. In the summer period, adult male movement was correlated only to total overall density ( $r = -0.95$ ,  $P < 0.01$ ). Adult female movement in the spring–early summer period showed no significant correlation with any variable, although breeding female density was almost significant ( $r = -0.78$ ,  $P < 0.10$ ). In summer, adult female movement was most strongly correlated with total overall density ( $r = -0.95$ ,  $P < 0.01$ ). Thus, at least in summer, high density may restrict movement and in the absence of resident breeding animals of the opposite sex, animals move more.

## DISCUSSION

The understanding of microtine social organization has improved considerably in the last 10 years, but the foundations of much of it still rests on observational, non-experimental work. Three sex ratio manipulations have now been carried out with the same general design on three different species: on *M. townsendii* (Redfield, Taitt & Krebs 1978a), on *M. oregoni* (Redfield, Taitt & Krebs 1978b), and our study on *M. pennsylvanicus*. A comparison amongst these would be useful to determine if any generality emerges. There were differences between the studies in the way they were conducted. In the first two studies, an attempt was made to manipulate populations towards either 20% or 80% males, whereas we manipulated populations towards 0% or 100% breeding males. We did not remove nonbreeding animals of the rare sex. In addition, in the first two studies, new animals of the abundant sex were introduced into the experimental populations continuously and these were obtained from the other experimental population from which they were removed (i.e. males removed from the female grid were introduced onto the male grid). Finally, in the analysis of the first two studies, no attempt was made to distinguish between the survival and recruitment of adults, sub-adults, and juveniles. It is unlikely that breeding adults and nonbreeding animals would show the same response to these manipulations. However, at least in *M. townsendii*, the majority of the animals caught appear to have been adults (C. J. Krebs, unpublished and, in addition, compare the numbers in the survival data of the control grid of Redfield, Taitt & Krebs (1978a, Table 2) with that

of juveniles and sub-adults of the same control grid of Taitt & Krebs (1981, Table 3)). However, lumping all age classes into one category increases the noise in the system and decreases the ability to detect responses when they occur. Thus, differences in results among the studies may originate from differences in techniques and analyses.

If breeding density is set by females as Boonstra (1977) predicts, then removal of the breeding males should have no influence on female survival, whereas removal of breeding females should decrease male survival. Conversely, if breeding density is determined by both sexes in a sex-specific manner as Redfield, Taitt & Krebs (1978a) predict, then the absence of one sex should not influence the survival of the remaining one. In our study, males did survive more poorly in the absence of females but females survived equally well in the presence or absence of males. Thus, the predictions of Boonstra (1977) are supported. However, the density of females on the Female grid were consistently lower than those on the Control, and if they were competing for space, these females should have survived better since they had more. They did not. But adult female survival was high on both areas (averaging 0.91 per 2 weeks on the Control and 0.90 per 2 weeks on the Female grid) and it is unlikely that survival in breeding females can be raised much above this. In *M. townsendii*, the survival of neither males nor females was affected by the presence or absence of the opposite sex and these results are consistent with the predictions of Redfield, Taitt & Krebs (1978a). However, neither sex was affected by the lower density of the same sex, which is contrary to both sets of predictions. In *M. oregoni*, the survival of both sexes appeared to be independent of the density of either one of them. The survival of males was consistently higher on both male and female grids than on the control, even though the male density on the control was only one-half to one-seventh that on the experimental grids. The survival of the females on the male and female grids was either similar to or higher than that on the control grid, even though female density on the control was one-third to approximately equal that on the experimental grids. Neither set of predictions was satisfied by these results.

With respect to recruitment, Redfield, Taitt & Krebs (1978a) predict that more recruits of the rare sex should enter the experimental grids. Similar predictions would logically follow from the hypothesis of Boonstra (1977) with the provision that since males were expected to compete for females and since there were no resident breeding females on the Female grid, recruitment by other males should be less restricted. In *M. pennsylvanicus*, greater recruitment occurred to the experimental grids than to the Control, it favoured the rare sex (at least during the main breeding season in spring-early summer), and more males entered the Male grid than the Control by at least a factor of two times in spring-early summer and by a factor of three to ten times in summer. In *M. townsendii*, more male recruits entered the control grid than entered the male or female grids, and equal numbers of female recruits entered the control and male grids, but lower numbers entered the female grid. Thus, neither male nor female recruitment was restricted onto the control grid (relative to the male or female grids though it was restricted relative to a total removal grid), but female recruitment may have been restricted to the female grid in 1973. However, this is questionable. They point out that part of the reason for the lower recruitment onto the female grid (thirty-four females) compared with that onto the control grid (sixty-one) was largely the result of only six sub-adult females entering the female grid compared with twenty-eight sub-adults entering the control grid. This may be a direct consequence of having only seven females on the female grid from March to May (when breeding was occurring) compared with twenty-two females on the control grid. During the rest of the breeding season, densities were similar. In *M. oregoni*, over two times as many

male and female recruits entered each of the experimental grids as entered the control grid. Thus, not only was there increased recruitment of the rare sex onto the female or male deficient grids, but an increased recruitment of the abundant sex occurred as well. Thus, among the three species studied, only *M. pennsylvanicus* responds as predicted by Redfield, Taitt & Krebs (1978a), with the exception of substantially greater recruitment of males onto the Male grid which follows from the predictions of Boonstra (1977).

What are the possible explanations for these obviously very different results among the three species? Only *M. pennsylvanicus* responded as Boonstra (1977) predicts and partially as Redfield, Taitt & Krebs (1978a) predict. The other two species for the most part, fit neither set of predictions. The first possibility, which we reject, is that the social organization of these species is indeed very different, and hence the results should be accepted at face value. The second possibility, which we find more acceptable, is that the experimental differences between the studies and conditions unique to some of them were responsible for the results. First, there were obvious differences in the way the studies were conducted and the data analysed as we indicate above. Second, Redfield, Taitt & Krebs (1978a) mention that if they were to repeat the experiment, they would not transfer animals from one experimental grid to another because many of these disappeared and their introduction may have caused distribution of the social structure. Third, the experimental populations in both *M. oregoni* and *M. townsendii* were not replicates of the control populations, even at the start of these studies. The experimental *M. oregoni* populations were about twice as dense as that of the control population throughout the study and this may have accounted for recruitment rates to them that were also double those of the control. The initial experimental *M. townsendii* populations were less than half as dense as that on the control and this condition persisted for the first half of the study. Differences in habitat amongst the grids may be part of the explanation. Hawes (1975) reported that *M. oregoni* is more commonly found in wetter habitats. In addition, the possibility that competition between the two species (Hawes 1975) accounted for some of these differences cannot be discounted, in spite of the covariance analysis in Redfield, Taitt & Krebs (1978b). In their experimental design, the male grid for *M. oregoni* became the female grid for *M. townsendii* and vice versa. Sullivan & Krebs (1981) report that *M. oregoni* populations cycle in numbers only in habitats where the larger *M. townsendii* is absent. Finally, the results obtained by Boonstra (1977) on *M. townsendii*, on an area where there were no *M. oregoni*, are inconsistent with those obtained by Redfield, Taitt & Krebs (1978a). Boonstra (1977) found that in experimentally produced low density populations, female survival always improved over that on the control area, whereas male survival improved only if cropping was carried out well before the onset of the breeding season. Redfield, Taitt & Krebs (1978a) found that survival was not improved under low density conditions. The above arguments lead us to suggest that the social structure of both species may still be similar to *M. pennsylvanicus*.

The last prediction of the sex-specific dispersed social system of Redfield, Taitt & Krebs (1978a) was that the movement and home range of the rare sex should be increased relative to that of the control, whereas the unmanipulated sex should have similar movement patterns to that on the control. From the proposal of Boonstra (1977), removal of females should result in greater movement of the males, both on and off (dispersal) the grid. Females should not be affected by the absence of males. Of the three studies, only ours addresses this question and only the movements of the unmanipulated sex could be calculated. Movements of the unmanipulated sex were always greater than those on the Control (Table 5). Generally, though not always, numbers of the unmanipulated sex were

less than those on the control grid in the main portion of the breeding season (spring and early summer) and thus reduced density may account for greater movements. Thus the predictions of Redfield, Taitt & Krebs were supported. However, there were two periods (August 1979 and 14 July to 29 August 1980) when breeding male densities on the Male grid exceeded those on the Control, yet movements on the Male grid were significantly greater than those on the Control grid. This evidence is consistent with the idea that spacing behaviour in males is female dependent and in their absence, competition is likely to be less severe. Many of the males on the Male grid obviously dispersed off the grid (Table 3), but the dispersal rate was not consistently higher in every year than that from the Control. Male survival, however, was consistently lower on the Male grid. This suggests that a greater proportion of these males were either dying *in situ* or were dispersing from the Male grid but not moving onto other trapping grids when they did move. Though female movement did increase on the Female grid, it was not accompanied by either poorer survival rates (Table 1) or higher dispersal rates (Table 3). Thus movement was not related to dispersal in females. Why females at reduced densities should move more is unclear if it has no direct demographic consequences. In summary, the evidence indicates that increased female movement was simply a response to density, while increased male movement was strongly related to the absence of females.

What determines the maximum number of breeding male *M. pennsylvanicus* on an area with a normal complement of females? The maximum number of breeding males occurring on the Control grid was set early in the spring in both 1980 and 1981, years in which densities were high. Only in 1979, a year of low initial spring density, was the maximum number of breeding males reached much later in the breeding season, in mid-summer. This suggests that at the onset of breeding in the spring in this study, breeding density was determined by the number present: the more males present initially, the more that actually remained. A similar relationship has been found in at least one bird species (Smith *et al.* 1981). After the spring reorganization in voles, entry of strange breeding males is determined by permeability of the social structure. Permeability can be defined as the ease of entry of a strange vole into a resident population. Populations at low densities (1979) are more permeable than those at high densities (1980 and 1981). However, the maximum male breeding density in 1979 was approximately half that in 1980 and 1981, even though large numbers of males were potentially available (Table 4). This suggests that after the social system has been established in the spring, the males present are able to control larger areas and leave fewer spaces for other males. This system may be analogous to that found in some birds. Removal of a number of territorial holders results in almost instantaneous replacement by a similar number of individuals (Watson & Jenkins 1968; Krebs 1971). However, when entire populations are removed, a greater number of replacements occupy the same area, with each pair occupying a smaller area (Knapton & Krebs 1974). The recruitment to the breeding male population of meadow voles, whether synchronously, as occurs at the onset of the breeding season, or asynchronously, as occurs throughout the rest of the breeding season, may be a major determinant of the maximum breeding density in normal populations where females are present. However, the presence of females are a necessary prerequisite for normal male spacing behaviour. In the absence of breeding females we found breeding male density on the Male grid exceeding that on the Control grid every year for part of July and August (Fig. 3) (i.e. in 1979 a maximum of twenty-two more males were found on the Male grid; in 1980, between nine and fourteen more males were present from the period from 2 July to 29 August; in the last trapping session in 1981 on 15 July, ten more males were present), lower survival of adult males on

the Male grid compared with those on the Control (Table 1), and greater recruitment of males onto the Male grid compared with the Control (Table 4).

Radiotelemetry studies have shown that males are not territorial since they do not occupy mutually exclusive home ranges (Madison 1980; Webster & Brooks 1981). Our evidence indicates that, because recruitment was restricted, there must be a limit to home range overlap in males. Exactly how the males whose home ranges overlap respond to each other and to strangers is not clear, but wounding is frequent in breeding voles and lemmings and is usually restricted to males (Krebs 1964; Christian 1971; Lidicker 1973; Rose & Gaines 1976; Krebs & Boonstra 1978; Rose 1979; R. Boonstra, unpublished). Possibly, the reaction of neighbouring males is similar to that described by Healey (1967) for *Peromyscus maniculatus* Wagner, in which aggression between neighbours is reduced but aggression towards strangers is high. In a similar manner 'dear enemy recognition' may also occur in meadow voles (for a recent summary in other species see Jaeger 1981).

The evidence suggests that the following is the most probable explanation for the basic social system of *Microtus pennsylvanicus* and microtines that have a similar polygamous mating system. We recognize that it will not apply to all microtines such as *M. ochrogaster* Wagner, which appear to be monogamous (Thomas & Birney 1979; Getz, Carter & Gavish 1981) or perhaps to species which occupy very patchy habitats such as *M. xanthognathus* Leach (Wolff 1980). However, studies which infer male territoriality from trapping data rather than from the more precise techniques like radiotelemetry (Madison 1980), may be in error because the results are highly dependent on trapping intervals, trap placement, and entry of the vole into the trap. Males do not directly defend resources essential to females, but rather form dominance hierarchies in which high ranking males obtained greatest access to oestrus females. Males are thus polygamous. These hierarchies are composed of groups of familiar males, whose home ranges overlap, and who are less aggressive towards each other, than towards strangers. Thus nonresident breeding males have little chance of entering an intact group of resident males. The formation of these hierarchies is probably dependent on density and at very low densities, the type of social system may be more territorial. Females compete only with other females for nest sites and space in which to raise young and thus occupy territories from which they exclude other breeding females.

Since male-male competition is expected to be intense in such a system, there should be sexual selection for traits which confer an advantage in the breeding hierarchy (Emlen & Oring 1977). One of these traits is body size, and meadow voles are sexually dimorphic for this characteristic. Mature males weigh about 7-10 g (about 20%) more than females. For example, at the onset of the breeding season in April 1980, overwintered males had a mean weight of 52.4 g ( $n = 64$ ) compared with a mean weight of 43.5 g ( $n = 91$ ) in females on the Control grid. In addition, males that remained on the grid tended to be significantly heavier than those disappearing from it at the onset of the breeding season (R. Boonstra, unpublished). Those animals that disperse from a population should have characteristics that have put them at a disadvantage with respect to the residents, e.g. lower body weight, maturation at a lower weight, and subordinate behaviour (Myers & Krebs 1971; Krebs *et al.* 1976; Krebs, Redfield & Taitt 1978; Boonstra & Krebs 1979; Krebs 1979; Beacham 1981). Gipps *et al.* (1981) indirectly also supported the dominant role played by heavyweight males, for when the voles were given scopolamine to make them less aggressive, the population showed a lower rate of loss. Gipps *et al.* suggested that those males normally driven from the population were now not forced to do so.

There is very limited evidence that dominance hierarchies between males may occur.

Webster & Brooks (1981) observed one case in which an oestrus female meadow vole came into contact with four males, but only one of these remained near the female and drove the others away. Caplis (1977), from observations on paired encounters in the laboratory of males caught in the field, found that males were less aggressive to strangers than to neighbours. Kalela (1957) and Viitala (1977) have observed instances in *Clethrionomys rufocanus* (Sund.) where numerous males chase and attempt to copulate with an oestrus female, though it is unclear whether a dominance hierarchy occurred among the males. Kalela (1957), Koshkina, Okulova & Aristova (1972), and Viitala (1977) also claim that there are dominance-subordinate relationships among males. Though Mihok (1979) found limited evidence that prior experience may result in behavioural dominance, he could find no evidence of long- or short-term associations in *C. gapperi* Vigors.

The spatial relations among female microtines appears to be more simple than in males. Breeding females tend to occupy mutually exclusive territories which show little overlap with territories of other breeding females (Mihok 1979; Madison 1980; Webster & Brooks 1981). They restrict recruitment of other breeding females (Table 3), and if sufficient numbers of them are removed, the survival of the remainder improves (Boonstra 1977). Why should this spatial arrangement occur? We suggest that females compete for the resources which maximize their own fitness—a nest site and space to promote growth and survival of their young. How much space is required by females? This will depend on the quality of the environment and this may be improved by the addition of such things as food (Taitt & Krebs 1981) and cover (Taitt *et al.* 1981). In our study, we found that breeding female density was generally lower on the Female grid than on the Control, but that survival was not improved above that on the Control (Table 1). Lower female densities were probably due to two factors: slightly poorer habitat on the Female grid (it was lower at one end and subject to flooding) and it suffered more from the severe winter weather of 1978–79, possibly because it did not have snow tunnels whereas the Control did. The similar high survival rates on the Control and Female grids indicate that the basic space requirements of the females were probably being met and that the low mortality rates were related simply to the costs of reproduction and not to competition. Breeding females appear instrumental in determining juvenile survival (Boonstra 1978; Getz *et al.* 1979; Taitt & Krebs 1981) and recruitment (Redfield, Taitt & Krebs 1978a) and thus mutually exclusive territories may have evolved to prevent other females from harming the young. These territories may also have evolved to prevent infanticide by other females or pregnancy failure and infanticide by strange males (Mallory & Brooks 1980; Webster, Gartshore & Brooks 1981), though there is no field evidence for the former, and the latter do not appear to be significant in the field (Boonstra 1980). However, females may not always be exclusive in their use of space at all times of a population fluctuation. Reich (1982) found in an analysis of double captures of *M. pennsylvanicus*, that breeding females were caught together more frequently than would be expected by chance and that pairs of females co-occurred more frequently in months of population increase than in months of population decrease. In addition, one of us (R.B.) has observed one instance of two females from a low density population in the field raising their young in a common nest. However, it was not possible to establish the genetic relatedness of these females.

The type of social system we propose would have profound implications for population regulation. Microtine rodents are characterized by marked fluctuations in population size (Krebs & Myers 1974; Krebs 1978) and one of the proposed explanations is the

genetic-behavioural hypothesis of Chitty (1967). If breeding is restricted to relatively few males who are socially dominant, then rapid genetic change in the population could occur. Even if there is less restriction of breeding by dominants as suggested here or if multiple paternity does occur (Birdsall & Nash 1973; Hanken & Sherman 1980), it is possible that the males who do the breeding are more similar genetically to each other, than they are to those that are excluded from the population (Myers & Krebs 1971). The result would still be non-random mating.

The present study suggests several areas that should be explored further. The essential question that must be asked is: How does the social structure of the species translate into the production of viable offspring which contribute to the next generation? With respect to the first portion of this question, we still have little definitive field evidence on many species as to what the social structure is and which sex sets breeding density. Two areas require intensive field investigation: radiotelemetry studies of the type pioneered by Brooks & Banks (1971) and Madison (1980) to infer in a detailed manner the interactions between individuals and perturbation experiments of the type pioneered by Redfield, Taitt & Krebs (1978a, b) to try to sort out the implications of these interactions. With respect to the second portion of the question, parentage of litters should be determined either by electrophoresis or by radioisotope techniques (R. H. Tamarin, unpublished) to isolate who is doing the breeding and what the characteristics are that promote successful breeding. A second question is: What are the characteristics of the environment or the animal itself that promote different social systems? In microtines, there may be a social system continuum ranging from a strictly monogamous situation, to one in which male territoriality and female polygyny occurs, to one in which male dominance hierarchies and female polygyny occurs. Exactly how species which are monogamous would respond to the type of manipulations reported in this paper would depend on which sex is more attached to the breeding site. If females are more site attached, we would predict similar responses to those found in this study with respect to survival and recruitment.

#### ACKNOWLEDGMENTS

We thank Ken Fukumoto, Moon Chow, Cathy Filkin, Larry Harrison, Kim Saunders, Julie Towers, Peter Fetterolf, Jim Ross, Pierre Blais, Bo-Kai Chow, Samuel Wong, Mike Dallman, Marc von der Gonna, and Carol Mashke for help with live-trapping, the Natural Sciences and Engineering Research Council of Canada and the Canadian National Sportsmen's Fund for generous support, and Dennis Chitty, Charles Krebs, and Steve Mihok for criticisms of the manuscript.

#### REFERENCES

- Beacham, T. D. (1981). Some demographic aspects of dispensers in fluctuating populations of the vole *Microtus townsendii*. *Oikos*, **36**, 273–280.
- Birdsall, D. A. & Nash, D. (1973). Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). *Evolution*, **27**, 106–110.
- 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. (1980). Infanticide in microtines: importance in natural populations. *Oecologia*, **46**, 262–265.
- Boonstra, R. & Krebs, C. J. (1978). Pitfall trapping of *Microtus townsendii*. *Journal of Mammalogy*, **59**, 136–148.

- Boonstra, R. & Krebs, C. J. (1979). Viability of large- and small-sized adults in fluctuating vole populations. *Ecology*, **60**, 567–573.
- Brooks, R. J. & Banks, E. M. (1971). Radio-tracking study of lemming home range. *Communications in Behavioral Biology*, **6**, 1–5.
- Bujalska, G. (1970). Reproduction stabilizing elements in an island population of *Clethrionomys glareolus* (Schreber, 1780). *Acta Theriologica*, **15**, 381–412.
- Bujalska, G. (1973). The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility*, Suppl. 19, 465–474.
- Caplis, P. (1977). *Neighbor recognition by the meadow vole (Microtus pennsylvanicus) and the role of olfactory cues*. Unpublished M.Sc. thesis, McGill University, Montreal, Canada.
- Chitty, D. (1967). The natural selection of self regulatory behaviour in animal populations. *Proceedings of the Ecological Society of Australia*, **2**, 51–78.
- Christian, J. J. (1971). Fighting, maturity, and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **52**, 556–567.
- Cohen, M. N., Malpass, R. S. & Klein, H. G. (Eds.) (1980). *Biosocial Mechanisms of Population Regulation*. Yale University Press, New Haven.
- Crook, J. H., Ellis, J. E. & Goss-Custard, J. D. (1976). Mammalian social systems: structure and function. *Animal Behaviour*, **24**, 261–274.
- Ebling, F. J. & Stoddart, D. M. (Eds.) (1978). *Population Control by Social Behaviour*. Institute of Biology Symposium 23, London.
- Eisenberg, J. F. (1966). The social organization of mammals. *Handbuch der Zoologica*, **10**(7), 1–92.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Getz, L. L., Carter, C. S. & Gavish, L. (1981). The mating system of the prairie vole, *Microtus ochrogaster*: field and laboratory evidence for pair bonding. *Behavioral Ecology and Sociobiology*, **8**, 189–194.
- Getz, L. L., Cole, F. R. & Gates, D. L. (1978). Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy*, **59**, 208–212.
- 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.
- Gipps, J. H. W., Taitt, M. J., Krebs, C. J. & Dundjerski, Z. (1981). Male aggression and the population dynamics of the vole, *Microtus townsendii*. *Canadian Journal of Zoology*, **59**, 147–157.
- Hanken, J. & Sherman, P. W. (1980). Multiple paternity in Belding's ground squirrel litters. *Science*, **212**, 351–353.
- Hawes, D. B. (1975). *Experimental studies of competition among four species of voles*. Unpublished Ph.D. thesis, University of British Columbia, Vancouver, Canada.
- Healey, M. C. (1967). Aggression and self-regulation of population size in deer mice. *Ecology*, **48**, 377–392.
- Iverson, S. L. & Turner, B. N. (1969). Under-snow shelter for small mammal trapping. *Journal of Wildlife Management*, **38**, 722–723.
- Jaeger, R. G. (1981). Dear enemy recognition and the costs of aggression between salamanders. *American Naturalist*, **117**, 962–974.
- Kalela, O. (1957). Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). *Annals. Academiæ Scientifiæ Fennicæ, Series A*, **34**, 1–60.
- Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39–69.
- Koshkina, T. V., Okulova, N. M. & Aristova, V. A. (1972). Territorial relationships in rodents and their role in the regulation of population density. *Transactions of the Moscow Society of Naturalists*, **48**, 215–237. Translated by S. Mihok, 1976.
- Knapton, R. W. & Krebs, J. R. (1974). Settlement patterns, territory size, and breeding density in the song sparrow (*Melospiza melodia*). *Canadian Journal of Zoology*, **52**, 1413–1420.
- Krebs, C. J. (1964). The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. *Arctic Institute of North America Technical Paper*, **15**, 104 pp.
- Krebs, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs*, **36**, 239–273.
- Krebs, C. J. (1978). A review of the Chitty Hypothesis of population regulation. *Canadian Journal of Zoology*, **56**, 2463–2480.
- Krebs, C. J. (1979). Dispersal, spacing behavior, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. *Fortschritte der Zoologie*, **25**, 61–77.
- Krebs, C. J. & Boonstra, R. (1978). Demography of the spring decline in populations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, **47**, 1007–1015.
- 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., Redfield, J. A., Taitt, M. J. & Hilborn, R. (1976). *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology*, **54**, 79–95.
- Krebs, J. R. (1971). Territory and breeding density in the great tit *Parus major* L. *Ecology*, **52**, 2–22.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen & Co. Ltd., London.
- 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.
- Leslie, P. H., Tener, J. S., Vizoso, M. & Chitty, H. (1955). The longevity and fertility of the Orkney vole *Microtus orcadensis*, as observed in the laboratory. *Proceedings of the Zoological Society of London*, **125**, 115–125.
- Lidicker, W. Z., Jr. (1973). Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecological Monographs*, **43**, 271–302.
- Madison, D. M. (1980). Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology*, **7**, 65–71.
- Mallory, F. F. & Brooks, R. J. (1980). Infanticide and pregnancy failure: reproductive strategies in the female collared lemming (*Dicrostonyx groenlandicus*). *Biology of Reproduction*, **22**, 192–196.
- Mihok, S. (1979). Behavioral structure and demography of subarctic *Clethrionomys glareolus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology*, **57**, 1520–1535.
- Myers, J. H. & Krebs, C. J. (1971). Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *M. ochrogaster*. *Ecological Monographs*, **44**, 53–78.
- 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 alterations of sex-ratios in populations of *Microtus oregoni*, the creeping vole. *Journal of Animal Ecology*, **47**, 55–69.
- Reich, L. M. (1982). *Some aspects of laboratory and field determined social behavior in Microtus pennsylvanicus*. Unpublished Ph.D. thesis, Boston University, Boston, U.S.A.
- Rodd, F. H. (1982). *A selective removal experiment on the meadow vole, Microtus pennsylvanicus*. Unpublished M.Sc. thesis, Toronto.
- Rose, R. K. (1979). Levels of wounding in the meadow vole, *Microtus pennsylvanicus*. *Journal of Mammalogy*, **60**, 37–45.
- Rose, R. K. & Gaines, M. S. (1976). Levels of aggression in fluctuating populations of the prairie vole, *Microtus ochrogaster*, in eastern Kansas. *Journal of Mammalogy*, **57**, 43–57.
- Smith, J. N. M., Montgomerie, R. D., Taitt, M. J. & Yom-Tov, Y. (1981). A winter feeding experiment on an island song sparrow population. *Oecologia*, **47**, 164–170.
- Sullivan, T. P. & Krebs, C. J. (1981). *Microtus* population biology: demography of *M. oregoni* in southwestern British Columbia. *Canadian Journal of Zoology*, **59**, 2092–2102.
- Taitt, M. J., Gipps, J. H. W., Krebs, C. J. & Dundjerski, Z. (1981). The effect of extra food and cover on declining populations of *Microtus townsendii*. *Canadian Journal of Zoology*, **59**, 1593–1599.
- 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.
- Thomas, J. A. & Birney, E. C. (1979). Parental care and mating system of the prairie vole, *Microtus ochrogaster*. *Behavioral Ecology and Sociobiology*, **5**, 171–186.
- Viitala, J. (1977). Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). *Annals Zoologica Fennicie*, **14**, 53–93.
- Watson, A. & Jenkins, D. (1968). Experiments on population control by territorial behaviour in red grouse. *Journal of Animal Ecology*, **37**, 595–614.
- Watson, A. & Moss, R. (1970). Dominance, spacing behaviour, and aggression in relation to population limitation in vertebrates. *Animal Populations in Relation to their Food Resources* (Ed. by A. Watson), pp. 167–218. Blackwell Scientific Publications, Oxford.
- Webster, A. B. & Brooks, R. J. (1981). Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62**, 738–751.
- Webster, A. B., Gartshore, R. G. & Brooks, R. J. (1981). Infanticide in the meadow vole, *Microtus pennsylvanicus*: significance in relation to social system and population cycling. *Behavioral and Neural Biology*, **31**, 342–347.
- Wolff, J. O. (1980). Social organization of the Taiga vole (*Microtus xanthognathus*). *The Biologist*, **62**, 34–45.

(Received 12 July 1982)