The spring decline in the meadow vole, *Microtus pennsylvanicus*: the effect of density

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The densities of six *Microtus pennsylvanicus* populations were reduced by removing large, sexually mature adults 6 months prior to (fall removal manipulation) and just prior to (spring removal manipulation) anticipated spring declines. When the spring decline on the control grid was a result of short distance dispersal, the manipulations had no effect; when it was a result of *in situ* mortality and (or) long distance dispersal, the fall removal manipulation produced a significant improvement in the survival rates of adult males. Adult female survival rates were high and unaffected by the manipulations. Adult reproductive rates were high and similar on all grids. The onset of the females' breeding season was advanced by the manipulations in two trials. Home range sizes were similar for all animals during the nonbreeding period. During the breeding period, males and females on the experimental grids had larger home ranges than those on the control grids.

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Les densités de six populations de *Microtus pennsylvanicus* se sont trouvées réduites à la suite du retrait de mâles adultes à maturité 6 mois avant (retrait d'automne) et juste avant (retrait de printemps) le déclin printanier prévu. Lorsque le déclin printanier dans la grille témoin était le résultat d'une dispersion sur une courte distance, les manipulations restaient sans effet; lorsque le déclin résultait de la mortalité *in situ* et (ou) d'une dispersion sur une grande distance, le retrait d'automne entraînait une augmentation significative des taux de survie des mâles adultes. Les taux de survie des femelles adultes étaient élevés et n'ont pas été affectés par les manipulations. Les taux de reproduction étaient élevés et semblables dans toutes les grilles. La saison de reproduction des femelles a été avancée par les manipulations dans les deux expériences. L'aire vitale était à peu près la même pour tous les animaux en dehors de la saison de reproduction. Durant la période de reproduction, les mâles et les femelles des grilles expérimentales avaient des aires vitales plus grandes que celles des animaux des grilles témoins.

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Introduction

Populations of voles and lemmings often experience extreme density fluctuations (Krebs and Myers 1974). Although the timing and length of the decline phase are variable, it is often associated with the onset of reproduction in the spring. Populations of many microtine and nonmicrotine rodent species experience spring declines, moderate losses in conjunction with the start of most breeding seasons (for example, Sadleir 1965; Chitty and Phipps 1966; Watts 1969; Flowerdew 1972; Krebs and Myers 1974; Fairbairn 1977; Krebs and Boonstra 1978). This suggests that the microtine crash could be an extreme case of the spring decline.

Several studies suggest that behavioural interactions cause the spring decline (Watson and Moss 1970; Turner and Iverson 1973; Boonstra 1977; Fairbairn 1977; Krebs *et al.* 1977; Krebs and Boonstra 1978). As the animals become more reproductive in the spring, they become more aggressive, breeding territories are established, and the population social structure is reorganized (Sadleir 1965; Healey 1967; Batzli and Pitelka 1971; Lidicker 1973; Turner and Iverson 1973; Rose and Gaines 1976; Fairbairn 1977, 1978; Boonstra and Rodd 1983). Survival rates fall as animals, many of them small and subordinate, are forced out of the population (Chitty and Phipps 1966; Turner and Iverson 1973; Fairbairn 1977, 1978; Krebs *et al.* 1978).

The relationships among population density, interaction rates, and the amount of aggression exhibited in a population are not well established. There is some evidence for increased social and aggressive encounter rates with increased densities (Southwick 1955; Bronson 1963; Bronson and Eleftheriou 1965; Vale *et al.* 1971; Lidicker 1973; Rose and Gaines 1976; Davis 1978; however, see also Pearson 1960; Batzli and Pitelka 1971; Davis 1978; Rose 1979). This evidence suggests that reducing the density of a population should decrease contact

rates and, in turn, increase survival rates.

This study tests the hypothesis that agonistic interactions cause spring declines in *Microtus pennsylvanicus*, the meadow vole. If intraspecific strife is responsible for the decline, reducing the number and intensity of interactions by reducing density should moderate or eliminate the spring decline. The densities of several *M. pennsylvanicus* populations were reduced in the spring, before the onset of reproduction and the attendant behavioural changes. A modified version of this experiment was performed on adjacent populations. The densities of these populations were reduced the previous fall, for two reasons. Conspecific interactions during the winter previous to a spring decline could be a factor contributing to that decline. Reducing population densities several months before the decline would determine the importance of those interactions and would also provide the residents with an extended time period to adjust to the new densities.

Materials and methods

This study was conducted at two sites near Toronto, Canada. One site, adjacent to the Toronto International Airport, was on abandoned farmland (see control and unmarked grids in the photograph in Boonstra and Rodd (1983)). The dominant grass species were *Poa pratensis*, *Poa compressa*, *Agropyron repens*, *Festuca pratensis*, and *Bromus inermis*. Other plants present included *Melilotus officinalis*, *Medicago lupulina*, *Geum macrophyllum*, *Solidago* spp., and *Aster* spp. Small mammals present on the grids were *Microtus pennsylvanicus* (meadow vole), *Peromyscus maniculatus bairdii* (deer mouse), and *Mus musculus* (house mouse).

The second site was 30 km north of Toronto, near Aurora. The control grid was on land that had recently been used as pasture. The dominant plant species were *Dactylis glomerata*, *Poa compressa*, *Phleum pratense*, and *Lotus corniculatus*. The experimental grids were on abandoned farmland about 2.4 km from the control grid. Plants on these grids included *Festuca pratensis*, *Festuca rubra*,

FIG. 1. The experimental design. Initiation of experimental density reduction ($\blacktriangle$) is shown.

Bromus inermis, and *Poa* spp. Small mammals that were captured regularly on all of the Aurora grids included *M. pennsylvanicus*, *M. musculus*, *Zapus hudsonius* (meadow jumping mouse), *Peromyscus leucopus* (white-footed mouse), *Blarina brevicauda* (big short-tailed shrew), and *Sorex cinereus* (masked shrew).

All grids had 100 trap points spaced 7.6 m apart in a 10 × 10 pattern. Each grid covered an area of approximately 0.7 ha (1.7 acres) and was at least 30 m from all other trapping grids. 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 (Pruitt 1959; Iverson and Turner 1969). Traps were baited with oats and provided with upholsterer's cotton for bedding.

Trapping was done in each area for a period of 1 day and two nights every 2nd week, weather permitting. Traps were set in the afternoon, checked the following morning, again in the afternoon, and a third time the subsequent morning. Traps were not reset for daytime trapping during the summer and trapping was limited to one night per trapping session in severe winter weather. Each vole was ear-tagged on first capture; its weight, sex, breeding condition, tag number, number of fresh rump wounds, and location on the grid were recorded at each capture.

Three complete trials of the experiment were done (Fig. 1). One complete trial of the experiment consisted of a control grid and two experimental grids: a fall removal grid and a spring removal grid. On the fall removal grid, the population was monitored for one or two trapping sessions in the autumn, and on subsequent sessions all but 50 selected animals were removed. Selected animals were young of the year that had not yet reproduced. Large, sexually mature individuals were removed since they are generally aggressive and hold dominant positions in the population (Turner and Iverson 1973; Mihok 1981); they presumably have a disproportionate influence on population processes. Body weight was used as an index of age where the reproductive history of an individual 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 living on the grid and those that occasionally visited the outskirts of the grid. Immigrant voles were removed as they were captured so that a low, constant density could be maintained. Just prior to the breeding season in the early spring, the population size was further reduced to about 35 individuals by removing animals selected randomly. When breeding began, all young animals (<33 g) were tagged and allowed to remain on the grid.

The population on the spring removal grid was monitored in the fall (except in trial 1 when trapping did not begin until March 1979), whenever weather permitted during the winter, and in the spring. In the spring, just before the start of the breeding season, all but 35 animals were removed. These animals were chosen randomly from among the resident individuals with histories comparable to those left on the fall removal grid. All large animals (>32 g) moving on to the grid after cropping began and those on the periphery of the grid were

FIG. 2. Population densities of *Microtus pennsylvanicus* during trial 1. The shaded area represents the nonbreeding period. Initiation of the cropping procedure is indicated with an arrow.

removed. New young animals (<33 g), assumed to have been born on the grid, were left on it. Since numbers were low on this grid during trial 1, all animals were allowed to remain.

We used weight as a rough estimate of age; animals were classified as adult (>33 g), subadult (22 to 33 g), or juvenile (<21 g). We defined these categories by summarizing data on all animals captured on both control grids during the breeding seasons and using them to estimate the median weight at which the voles reached sexual maturity (Leslie *et al.* 1945). Adults were generally in breeding condition, subadults were in transition from nonbreeding to breeding condition, and few juveniles were in breeding condition.

Animals that were chosen to remain on the experimental grids were probably born after the end of June and would share characteristics common to voles born at that time (Schwartz *et al.* 1964). However, individuals on the control grids in the fall were heterogeneous for age and season of birth. From among the control animals, we chose a group of individuals that were similar to those on the experimental grids on the basis of weight and reproductive history. We used this "control cohort" for the analysis of parameters that would be affected by age and season of birth: reproductive and survival rates, wounding, and home range size.

Results

Trappability

The direct enumeration method used in this study requires that a substantial proportion of the population is caught each trapping session (Hilborn *et al.* 1976). As an index of the "catchability" of the voles, the number of animals captured each trapping session was compared with the minimum number known to be alive using the equation for minimum unweighted trappability given in Boonstra and Krebs (1978).

The trappabilities for all populations in the fall and winter ranged from 27 to 78%, with the values for most grids falling between 50 and 75%. Trappability improved in the spring period and all populations had a trappability of at least 70% (except the trial 2 experimental populations (56%)). There were no consistent differences in trappability between the control and experimental populations.

Population density

At the beginning of each trial, the control populations were

FIG. 3. Population densities of *Microtus pennsylvanicus* during trial 2. The shaded area represents the nonbreeding period. Initiation of the cropping procedure is indicated with an arrow.

at high densities (228 to 469 voles/ha; Figs. 2, 3, and 4). The following spring, all control populations experienced declines. In trials 1 and 2, the declines were typical in that they lasted for approximately 2 months. In trial 3, the decline was more prolonged. Initially, densities on the experimental grids were similar to those on the control grids, given the lag time before voles on a new grid begin to enter traps. In every trial, after the manipulations, the experimental population densities were maintained at lower levels than those on the control, despite the high rates of immigration into the manipulated populations.

In trial 1, numbers on the control grid remained high (approximately 300 animals) from the start of the study in October until early January (Fig. 2). At that time, a substantial decline was initiated by severe weather conditions (freezing rain, which replaced the snow cover with a layer of ice, was followed by very low temperatures). In March and April, when weather conditions improved, the population on the control grid continued to decline because of dispersal (Boonstra and Rodd 1983). By the end of the spring decline, 67 animals were known to be on the grid. During the winter, the fall removal experimental cohort was maintained at approximately 70 animals. About 40 immigrant animals were removed from this grid each trapping session until the end of February. The low immigration rate during the spring suggests that the effects of the severe winter weather were widespread. This population declined to 23 animals by the end of April. Only nine individuals were caught on the spring removal grid when trapping began in March. The losses that this population suffered from

FIG. 4. Population densities of *Microtus pennsylvanicus* during trial 3. The shaded area represents the nonbreeding period. Initiation of the cropping procedure is indicated with an arrow.

TABLE 1. Mean wounding rates for adult males in reproductive condition during the breeding season (March–July). Numbers of adult males in reproductive condition are shown in parentheses

Grid	Trial 1	Trial 2	Trial 3
Control	1.4 (86)	1.7 (59)	1.8 (78)
Fall removal	1.6 (84)	1.1 (139)*	0.7 (103)*
Spring removal	1.3 (72)	1.4 (172)	1.0 (172)

* $P < 0.05$

the harsh winter may have been intensified by the poor vegetative cover on the grid at that time.

In trial 2, the control density rose steadily from October to March (Fig. 3). During the subsequent spring decline, about 40% of the population disappeared. The experimental cohort on the fall removal grid had between 50 and 65 animals during the winter. At least 30 immigrant voles were removed from the grid during each session between October and May. Further cropping in the spring and the disappearance of some animals reduced the population to a low of 27 in April. The spring removal population had 175 animals in March when the density manipulations were started. By the end of April, there were 35 animals on the grid. Approximately 125 immigrants were

TABLE 2. Mean minimum survival rates per 14-day period for adult *Microtus pennsylvanicus* during the breeding period (March–July). Numbers of voles known to be alive on the areas at the time sampled, summed over the period, are in parentheses

Grid	Trial 1		Trial 2		Trial 3	
	Male	Female	Male	Female	Male	Female
Control	0.805 (77)	0.811 (111)	0.741 (58)	0.898 (88)	0.816 (76)	0.878 (139)
Fall removal	0.758 (62)	0.866 (112)	0.811 (111)*	0.924 (145)	0.805 (82)	0.803 (71)
Spring removal	0.681 (47)	0.848 (33)	0.783 (115)	0.909 (175)	0.794 (73)	0.819 (72)

* $P < 0.05$

removed from this grid during the first 2 months after cropping began.

In trial 3, the control population size rose gradually from October to April (Fig. 4). It then declined steadily until the end of the study in early July. The initial density on the fall removal grid was approximately 90. The size of the experimental cohort was maintained at about 60 animals throughout the winter. About 35 immigrants were removed from this grid during each trapping session between December and mid-May. By the end of April, numbers had fallen to 22 as a result of death, dispersal, and cropping. The spring removal grid population increased throughout the winter to about 170 individuals by mid-March, when cropping began. Approximately 220 immigrants were removed from this grid during the first 2 months after cropping began. The resident population size was lowest, at 29 voles, at the end of April.

Wounding

The number of wounds per vole is used as an indication of the number of aggressive interactions between individuals (Christian 1971; Lidicker 1973; Turner and Iverson 1973; Rose and Gaines 1976); it was examined here to assess the effectiveness of the density manipulations for reducing the number of intraspecific aggressive interactions. Mean wounding rates were calculated only for adult males in reproductive condition (Table 1) as rates for all other categories were extremely low. Mean rates were calculated for the entire breeding period (mid-March to early July), since there was little wounding at the onset of the breeding season. Comparisons were made only among males resident on experimental grids and comparable cohorts on control plots. Differences were tested with the Wilcoxon's ranked sign test (Sokal and Rohlf 1973) because individuals could be included in the calculated rates for many weeks in succession. Males in trial 1 showed similar rates of wounding on all three grids. In trials 2 and 3, there were significantly fewer wounds per individual on the fall removal grids than on the control grids ($P < 0.05$). Levels on the spring removal grids and control grids were similar. Therefore, the density manipulations appeared to reduce aggressive interaction rates on fall removal grids when there were large differences between control and experimental grid densities.

Adult survival

We expected the density manipulations to decrease interaction rates and in turn increase survival rates. Minimum adult survival rates were determined by summing the numbers of animals captured and recaptured during the early portion of the breeding period (late March to early July) and calculating mean survival rates for 14-day periods (Table 2). This method of estimating survival rates does not distinguish between death on the grid and emigration. Survival rates of adults on the experi-

FIG. 5. Survivorship curves for adult male *Microtus pennsylvanicus* from the onset of reduced survival rates in the spring to the end of the study period. The control (●), fall removal (⊙), and spring removal (○) grids are shown. Sample sizes are given in Table 4.

mental grids were compared with those of similar-aged adults on the control grid ("control cohort"). As some individuals were included in the analysis several times, the Wilcoxon's ranked sign test was used (Sokal and Rohlf 1973). A cohort analysis was also used since both techniques required the loss of some information. The results of the Lee–Desu statistic for the cohort analysis (Hull and Nie 1979) were consistent with those of the Wilcoxon test.

Adult female survival rates were high on all control grids; they were also high on the experimental grids and there were

TABLE 3. Survival, dispersal, and disappearance rates for adult male *Microtus pennsylvanicus* during the spring decline period

	Control grid		Fall removal grid		Spring removal grid	
	A*	B†	A	B	A	B
Trial 1						
% remaining on grid at end of period	58	43	64	36	43	44
% that dispersed to neighbouring grids	21	36	7	57	0	28
% that disappeared but did not appear on neighbouring grids	21	21	28	7	57	28
Sample size	28	28	14	14	7	7
Trial 2						
% remaining on grid at end of period	77	54	100	91	80	63
% that dispersed to neighbouring grids	0	0	0	9	10	21
% that disappeared but did not appear on neighbouring grids	23	46	0	0	10	16
Sample size	13	13	11	11	19	19
Trial 3						
% remaining on grid at end of period	89	61	96	65	95	72
% that dispersed to neighbouring grids	0	17	0	13	0	0
% that disappeared but did not appear on neighbouring grids	11	22	4	22	5	28
Sample size	18	18	23	23	21	21

*A, first 2-week period after the onset of breeding.

†B, breeding period, including period A above (mid-March to early July).

TABLE 4. Intensity of adult breeding activity. Data are expressed as the percentage of *Microtus pennsylvanicus* individuals showing the given characteristic summed for the early part of the breeding season (April–July). Numbers of voles known to be alive on the areas at the time sampled, summed over the period, are shown in parentheses

Trial	Grid	Males with scrotal testes	Females	
			With perforate vagina	Lactating
1	Control	96 (88)	62 (152)	54 (152)
	Fall removal	92 (87)	64 (149)	65 (149)
	Spring removal	96 (74)	69 (49)	73 (49)
2	Control	93 (61)	62 (113)	59 (113)
	Fall removal	95 (144)	78 (198)	62 (198)
	Spring removal	93 (183)	74 (287)	57 (287)
3	Control	89 (84)	47 (166)	55 (166)
	Fall removal	89 (109)	54 (99)	45 (99)
	Spring removal	87 (184)	47 (119)	51 (119)

no significant differences between the rates for these animals and for those on the control grids. Male survival rates on the control grids were fairly high when averaged over the period. However, the survivorship curves (Fig. 5) that depict survival rates as they began to fall from high winter levels at the onset of breeding show that adult males suffered severe but brief spring declines in two trials. During the first 2-week period after the onset of breeding, 42 and 23% of the males were lost from the control grids in trials 1 and 2, respectively (Table 3). During subsequent weeks, survival rates improved considerably and remained fairly constant. Males on the control grid in trial 3 did not show a typical spring decline; they suffered steady losses throughout the period.

Although the declines of trials 1 and 2 appear similar, their mechanics were different. Of the individuals that belonged to the trial 1 "control cohort," more than half of those that disap-

peared dispersed to adjacent trapping grids. None of those that disappeared from the "control cohort" during trial 2 were later recovered on adjacent grids. These patterns held for both the severe 2-week declines and for the entire spring – early summer period. About half of the males that disappeared from the trial 3 control grid during this period dispersed.

Survival was significantly improved for males on the fall removal grid in only one of the three trials, trial 2 (Table 2). During this trial, none of the individuals that disappeared from the "control cohort" dispersed to neighbouring grids. Female survival was not improved on any of the fall removal grids. There were no differences between survival rates on the control and spring removal grids for any trial for either sex.

Reproduction

Breeding activity was estimated by examining external

FIG. 6. Effect of grid and sex on home range area. Response curves of (a) area versus sex and (b) area versus grid for breeding and nonbreeding periods. Mean areas in grid units (1 grid unit = 57.8 m²) are least square means. Vertical bars represent 1 SE on either side of the mean.

reproductive characteristics. For males, the position of the testes and for females, the condition of the vagina and the lactation tissue were used to indicate breeding condition. Obviously pregnant females and those with new litters in their traps were designated as breeding. Only voles selected to be residents on the experimental grids and comparable animals on the control grids ("control cohorts") were included in this analysis.

The influence of the manipulations on the timing of the onset of breeding was determined by examining differences in the date of the first spring trapping session during which at least 50% of the population was in breeding condition. The onset of male reproduction was unaffected by the manipulations. For females, in the first two trials of this study, perforation of the vaginal orifice was not affected by the experimental manipulations. In the last trial, the onset of this condition was advanced on the fall removal grid and retarded on the spring removal grid. Females began lactating soon after males became reproductive on all grids in the first two trials, except on the control grid in trial 1, on which lactation was delayed for 3 weeks. In trial 3, females were lactating 2 weeks earlier on the experimental grids than on the control grid. Thus both experimental manipulations advanced the onset of lactation in two trials.

The intensity of breeding activity was defined as the total number of reproductive individuals captured during a standard time period expressed as a proportion of the population size (Table 4). Adult female breeding was not affected consistently by the experimental conditions. In trial 1, more females on both experimental grids were lactating than on the control; in trial 2, more females on the experimental grids had perforate vaginæ; and in trial 3, fewer females on the fall removal grid were

lactating. The proportions of males in breeding condition were high on all grids and were similar within each trial.

Home range

We summarized live-trapping location data for 6-week periods and calculated rough estimates of home range size according to an elliptical home range model based on a bivariate normal distribution (Jennrich and Turner 1969; Mazurkiewicz 1971). Nonbreeding (late January to early March) and breeding periods (late April to early June) were analysed so that seasonal as well as experimental differences could be examined. Animals caught fewer than five times during the interval and those living near the edges of grids were excluded from the analysis. Only animals in the "control cohorts" were used in comparisons with animals resident on experimental grids. Home range areas were not calculated for the spring removal grids in trials 1 (both periods) and 3 (nonbreeding period) because capture sample sizes were small.

A three-way analysis of variance, with trial as a blocking factor, was done to examine the effects of grid, period, and sex on home range size. The SAS general linear model procedure was used because the design was unbalanced (Ray 1982). Type III sums of squares were appropriate and are presented in Table 5; least square means and standard errors are plotted in Fig. 6. Main effects, grid $\times$ period, and period $\times$ sex interactions were significant (Table 5).

During the nonbreeding periods, all voles used similar-sized areas, regardless of sex (Fig. 6a) and experimental manipulation (Fig. 6b). With the onset of the breeding period, when animals generally increase home range size (Getz 1961; Turner and Iverson 1973; Webster and Brooks 1981), males and

TABLE 5. Three-way analysis of variance on home range size, with trial as a blocking factor. A general linear model procedure was used for the analysis. Type III sums of squares are presented

Source	df	SS	F	P
Grid	2	4980	22.53	0.0001
Period	1	11500	104.31	0.0001
Sex	1	7150	64.75	0.0001
Trial	2	1040	4.75	0.01
Grid $\times$ period	2	1730	7.82	0.0005
Grid $\times$ sex	2	503	2.28	0.10
Period $\times$ sex	1	3930	35.62	0.0001
Grid $\times$ period $\times$ sex	2	233	1.06	0.30
Error	280	30900		

females on the control grids maintained ranges similar to those they held during the nonbreeding period (Fig. 6b). However, animals on the experimental grids did significantly enlarge their home ranges (Fig. 6b). As a result, animals on the experimental grids were using significantly larger areas than those on control grids (Fig. 6b). During this period, males on all grids had larger mean home ranges than females on the same grids (Fig. 6a; grid $\times$ sex interaction, $P > 0.05$).

During the breeding period, for both sexes, home range size was related to total adult density at the start of the breeding period (males: $r = -0.94$, $df = 6$; females: $r = -0.80$, $df = 6$).

Discussion

The control *Microtus pennsylvanicus* populations showed typical spring declines, with survival rates falling with the onset of the breeding season but improving several weeks later, in two trials of this study. Animals on the third control grid were lost steadily from the population throughout the winter, spring, and early part of the summer. Previous studies have found that this species often shows a sharp, short decline in the spring (Getz 1960; Golley 1961; Krebs *et al.* 1969; Tamarin 1977a, 1977b), although other patterns have been observed during the spring period (Getz 1960; Tamarin 1977a, 1977b).

In an attempt to elucidate the behavioural mechanisms responsible for the spring decline, densities of six experimental *M. pennsylvanicus* populations were reduced prior to the spring reorganization period. We assumed that agonistic interactions among voles would decrease and, as a result, various life history parameters would be modified and the spring decline would be moderated or eliminated.

We used number of wounds inflicted by conspecifics as an index of the level of aggression in the populations (Rose and Gaines 1976; Krebs *et al.* 1977). In this study, density manipulations aimed specifically at removing heavy, presumably dominant animals (Turner and Iverson 1973; Mihok 1981) decreased wounding rates on the fall removal grids in two trials. This suggests that extreme density reductions can cause a decrease in the agonistic interaction rate. However, wounding levels were not significantly reduced on any of the spring removal grids. The spring removal manipulation may have been less effective than the fall removal at reducing agonistic interactions for several reasons. The spring manipulations probably disrupted the social reorganization process and caused some strife. Also, the spring removal grid populations probably did not stabilize at the low fall removal levels before the breeding season began.

Large proportions of the adult males on the control grids were lost during severe but brief spring declines in two trials of this study. Adult male survival was improved significantly during this period by the fall removal manipulation in trial 2. During that trial, most of the males that were disappearing from the "control cohort" on the control grid were probably dying *in situ* because little dispersal was detected. The large difference between male and female survival rates on the control grid during that trial suggests that behavioural interactions, rather than some extrinsic factor alone, were primarily responsible for the control males' poor survival rates. When emigration from a population to nearby grids accounted for most of the reduction in male survival on the control grid, as occurred in the spring decline during trial 1, survival rates were not improved by the fall removal manipulation. Dispersal rates would have to be reduced to improve survival rates under these conditions, but the simple density manipulations done here did not significantly affect them.

During trial 3, the decline during the spring period was prolonged and much of the loss was a result of dispersal to neighbouring areas. Again, when poor survival on the control grid was a result of dispersal, the fall removal manipulation had no effect.

The evidence from this study suggests that, when behavioural interactions are severe enough to cause *in situ* mortality or dispersal over extremely long distances, removing the large, sexually mature individuals from a population can improve adult male survival rates. Other studies that directly manipulated the behaviour of a large proportion of the resident animals successfully improved adult male survival rates (Krebs *et al.* 1978; Gipps *et al.* 1981; Taitt and Krebs 1982). In studies similar to this one, adult male survival was improved by density manipulations (Smyth 1968; Krebs *et al.* 1969; Boonstra (fall cropped population) 1977). Unfortunately, dispersal rates were not examined in any of these studies. However, as in our study, male survival was improved primarily when survival on the control grids was poor (0.75 or less per 14 day period) (Smyth 1968; Boonstra 1977; however, see Krebs *et al.* 1969). Since other studies have found that little of the loss from a severe decline is a result of dispersal (Krebs and Boonstra 1978; Beacham 1980), this suggests that previous density manipulations improved survival rates only when dispersal was not an important component of the losses. Therefore, there appear to be at least two mechanisms responsible for the microtine spring decline and density manipulations affect only one of them.

The spring removal manipulation had no effect on adult male survival in any of the trials in this experiment. In the only other study that attempted this manipulation, adult male survival also was unaffected (Boonstra 1977). It was suggested that overwintered males do not respond to spring population manipulations because they have been "programmed" to decline before the manipulations have been completed (Boonstra 1977; Krebs and Boonstra 1978). Boonstra (1977) also suggested that spring cropping disrupted the social structure that had been developing in the early spring and, after the cropping, some males were left without females in their home ranges. Few males remain in areas devoid of females (Boonstra and Rodd 1983). Also, animals in the new, unstable social structure would find it more difficult to drive out the intruders that entered the population during the cropping (Fairbairn 1978). These factors could have caused dispersal and thus reduced survival rates (Nowak 1971). However, it could also be argued that animals

on spring removal grids had already destroyed some aspect of their environment, such as their food supply, and could not benefit from reduced densities. The addition of food and cover to experimental grids has had varied success, from no effect to a significant increase in adult survival rates (Krebs and Delong 1965; Cole and Batzli 1978; Gilbert and Krebs 1981; Taitt *et al.* 1981). All of these factors must be considered when further spring manipulation work is done.

Adult female survival rates were high on all of the control grids and they were not affected significantly by either of the density manipulations. Adult female survival rates were generally unaffected by the experimental conditions in other studies (Smyth 1968; Krebs *et al.* 1969). However, they were improved in both fall and spring removal experiments in another study where control females had poor survival rates (Boonstra 1977).

Adult female reproductive condition was not affected consistently by the density manipulations. More females were lactating in one trial than on the control, fewer in another, while more had perforate vaginae in the third. The onset of female reproduction, as shown by the proportion lactating, was accelerated on both grids in two trials. Adult males experienced uniformly high breeding rates and appeared to be unaffected by the experimental procedures.

Most density manipulation studies have only affected adult reproduction marginally (Krebs 1966; Watts 1970; Boonstra 1978; Krebs *et al.* 1978); in one case, a larger proportion of the females were lactating on experimental grids (Krebs *et al.* 1969). Apparently, adult reproduction does not respond well to this type of manipulation. The advancement of the female breeding season in this study and the one done by Krebs *et al.* (1969) might have been due to increased availability of food (Gilbert and Krebs 1981).

During the winter, when few voles were in breeding condition, all individuals had similar-sized home ranges, regardless of sex and experimental condition and despite relatively high densities on the control grids. This result was not unexpected, since nonreproductive voles are more gregarious, less active, and use smaller areas than reproductive ones (Frank 1957; Getz 1961; Turner and Iverson 1973; West 1977; Webster and Brooks 1981; Wolff and Lidicker 1981).

On control grids in this study, home range expansion with the onset of breeding was minimal, despite the fact that range expansion in the spring is a characteristic feature of microtine biology (Getz 1961; Kikkawa 1964; Turner and Iverson 1973; Ferns 1978; Webster and Brooks 1981). However, animals on the experimental grids enlarged their home ranges in the spring to areas significantly greater than those used on the control grids. These results suggest that home range size, for both sexes, is regulated by population density; as densities decline, home range size expands until all available space is filled or some upper size limit is reached. Some workers have reported negative correlations between home range length or area and population density for a variety of small rodent species (Bendell 1959; Stickel 1960; Krebs 1966; Van Vleck 1969; Koshkina and Korotkov 1975; Rose 1979; Abramsky and Tracy 1980; Gaines and Johnson 1982). However, general density reduction studies had no effect (Krebs 1966) or produced only a slight increase in adult movements (Boonstra 1977).

The fall and spring removal manipulations produced essentially the same changes in home range size and female reproduction. Neither manipulation had an effect on female

survival or on male reproduction. Only male wounding and survival rates were affected by the fall removal manipulation but not by the spring manipulation. These differences could be a result of physiological or psychological changes that occurred in males before the spring manipulations were done or some artifact of the manipulations.

To summarize, it is possible to reduce the number of aggressive interactions between conspecific males by removing a large proportion of the large, sexually mature individuals from a population well in advance of the spring breeding period. When males are forced to move during a spring decline from a control population to neighbouring areas by social and (or) physical factors, this experimental manipulation does not affect an individual's propensity to disperse. However, when they are experiencing a more severe situation and they are dying *in situ* or moving over long distances, this type of density manipulation alters their environment, they are able to remain in the population, and the spring decline is moderated.

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