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EFFECT OF CONSPECIFICS ON SURVIVAL DURING POPULATION DECLINES IN *MICROTUS TOWNSENDII*

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INTRODUCTION

Intraspecific behavioural interactions are believed to be critical in the regulation of many animal populations (Watson & Moss 1970). Despite over 40 years of research, the methods by which microtine populations are regulated is still unknown (for a review, see Krebs & Myers 1974). The extrinsic hypotheses of disease (Findlay & Middleton 1934; Chitty 1954), food and nutrients (Pitelka 1964; Schultz 1969), predation (Pearson 1966, 1971), and weather (Fuller 1969) have all been unsuccessful in providing necessary causes of cycles. The most promising explanation to account for the characteristic changes that occur in reproduction, mortality, dispersal, and growth is that behavioural interactions between animals are causing the fluctuations (Krebs & Myers 1974).

In this study, I have attempted to test part of Chitty's (1967) hypothesis that behavioural interactions are responsible for the decline. The secretive behaviour of voles demands that indirect methods be used to test the association of behaviour with population change in field experiments. My experiments are based on two critical assumptions: first, that the significant agonistic interactions are a function of the number of contacts between individuals in a field population; and second, that the number of contacts between individuals is related to population density in some positive manner. Given these two assumptions, I predicted that a drastic reduction in population size during the decline should decrease the rate of contact between individuals, and hence increase the survival rate of the remaining adults and their offspring. I report here a series of field experiments on *Microtus townsendii* (Bachman) in which I created low density populations by cropping during and before population declines.

STUDY AREA

The study was carried out on Westham Island in the delta of the Fraser River, near Vancouver, British Columbia, on a 37-acre (15 ha) parcel of pastureland owned by the Department of National Defence. Grid I, which was used as the control in the experiment of LeDuc & Krebs (1975) and had been trapped since July 1971, was used for the same purposes in the present study (Fig. 1).

The study area was a relatively flat grassland, which has had grass on it since 1946 and has not been grazed since 1963. An aerial photograph of the area can be found in LeDuc & Krebs (1975). The dominant plants on the four grids are shown in Table 1. The percentage of cover was determined by the use of 1 × 1 m plots at each trap point. There was a great

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FIG. 1. Map of the study area on Westham Island. The control area was grid I; the experimental areas used in this study were grids L, X, and Z; grid G was an experimental grid used in another study.

deal of variability between grids, with *Agropyron repens* (L.) Beauv. dominating grids L and Z and *Agrostis alba* L. dominating grids I and X. However, grass cover dominated the vegetation on all grids, always accounting for more than 90% of the cover. Few herbaceous species occurred; creeping thistle (*Cirsium arvense* (L.) Scop.) was the most common.

Table 1. Percentage cover of four trapping grids on Westham Island, 1974

	Grid I	Grid L	Grid X	Grid Z
<i>Agropyron repens</i>	27	52	20	42
<i>Agrostis alba</i>	58	22	55	28
<i>Holcus lanatus</i> L.	2	4	10	15
<i>Phleum pratense</i> L.	1		1	1
<i>Poa pratensis</i> L.	9	7	11	11
<i>Cirsium arvense</i>	2	7	2	2

METHODS

Two experimental designs were used (Table 2). Spring reductions were carried out on two grids during 1973 and on one grid during 1974. Spring reductions involved cropping the population during the spring decline in numbers. Autumn reductions were carried out on two grids during 1973–4. Autumn reductions involved cropping the population throughout the fall and winter before the spring decline in numbers. Details of these manipulations for each grid listed in Table 2 are given in Boonstra (1976).

Each trapping grid except grid L had 100 trapping points arranged in a 10×10 pattern (Fig. 1). These areas were approximately 1.7 acre (0.7 ha) in size. Grid L was an irregular trapping area with sixty-eight trapping points and an area of 0.9 acre (0.4 ha) bordered on one side by a drainage ditch and on the other by a dirt road. Each trapping point was 7.6 m (25 ft) from the next. Longworth live-traps were placed at every station and baited with oats; cotton bedding was provided. Additional traps (up to fifty) were added to the control grid as density increased. On all other grids only one trap per station was used.

Table 2. *Summary of methods used on the experimental grids*

Grid	March–April 1973	Summer 1973	Autumn 1973	Winter 1973–1974	March 1974
X	Removed all but 20 animals; removed all new recruits	All animals allowed to remain	Removed all old and new adults; young allowed to remain	Removed all but 28–30 of the autumn young	
L	Removed all animals; introduced 24 animals from X	Same as X	Removed all animals except pregnant females and some introduced pregnant females from X; only young from these females allowed to remain		
Z					Removed all but 20 animals as on X, spring 1973

Traps were generally 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 (occasionally a 1-week trapping interval and once a 3-week trapping interval were used). During the summer, traps were set only in evenings to avoid mortality in traps during the heat of the day.

All voles were ear-tagged, and on each capture the following data were recorded: trap location; sex; sexual condition (for males position of the testes and for females vagina perforate or not; nipples small, medium, or large; pubic symphysis closed, slightly open, or open; pregnant or not); and weight. Animals were classified as adult (≥ 43 g) or young. Few juveniles were caught so that no distinction was made between subadults and juveniles.

I have attempted to enumerate the population in this study, since it is not possible to sample *Microtus* populations randomly (Krebs 1966). This method of demographic analysis requires that a large proportion of the individuals of trappable age be captured every time. The trappability of the population was calculated by the method of Hilborn, Redfield & Krebs (1976). During the autumn, winter, and spring trappability was always high, ranging from 82–91% on the control grid. There were no differences in trappability between the sexes. Experimental grids also had high trappabilities ranging from 74 to 90%. In the summer, trappability on the control remained above 82% while that on grids L and X was approximately 10–15% lower. This was probably related to greater competition for traps on grids L and X than on the control grid, where fifty more traps were used. I believe, therefore, that the demographic statistics obtained from these data are accurate for adults. Young voles are less trappable than adults and are under represented in my samples.

RESULTS

Population density

The population on the control grid decreased at an average rate of 8% per week from December 1972 to May 1973 (Fig. 2(a)), increased by 4% per week from May to September, and by 6% per week from September to December. During early 1974, the population again declined, falling at an average rate of 11% per week to reach a low in April. The rate of loss of males in the late winter and spring was generally more rapid than that of females (2–3% more per week) but the rate of gain during the summer and fall was also more rapid by the same amount.

When setting up grids X and Z, I had hoped that the populations on them were comparable to those on the control. Before the first reduction, seventy-three animals were caught on grid X compared with ninety-two on the control grid. Grid X had been prebaited for 4 weeks prior to the first removal. In 1974, seventy-eight animals were

Table 3. *Average numbers per 0.7 hectare (1.7 acre) grid after removal on the experimental grids. Density on grid L was corrected for area. The percentage that these made up of control densities is given in parentheses*

Grid	Spring 1973	Summer 1973	Sept.–Dec. 1973	Jan.–March 1974	March–April 1974
L	26 (32%)	93 (121%)	51 (30%)	55 (40%)	
X	30 (41%)	68 (88%)	66 (39%)	32 (24%)	
Z					22 (32%)

caught on grid Z in the first trapping session compared with 110 animals on the control in the same week. Grid Z had been prebaited for 2 weeks prior to the first removal. Because some animals may require more time to get used to traps, densities on these two grids were probably reasonably similar to those on the control. Therefore, these grids were good experimental areas.

The cropping procedures in spring 1973 and spring 1974 were effective in maintaining densities considerably below those on the control grid (Table 3 and Fig. 2 (a) and (b)). In 1973, after the cropping stopped, the population on grid X quickly built up (averaging 12% gain per week) to reach 103 animals in July. It then stayed at approximately this number for the rest of the summer. From September to December, a total of 163 adult residents and recruits were removed from grid X, but the densities of young continued to increase. In the next 3½ months an additional 210 animals were removed from grid X. From late March onward, numbers on X started increasing because of recruitment of young of the year. Throughout the autumn, winter and spring of 1973–4, grid X had densities that were 1/4–2/5 that on the control.

On grid L (Fig. 2(b)), after cropping ceased in 1973, density quickly increased to become comparable to that on the control. However, this grid showed a mid-summer drop in numbers that was not evident on grid X and only occurred in one trapping session on the control grid. During the fall, a total of eight pregnant females was introduced on to grid L from grid X. These individuals plus the young from approximately eight pregnancies from female residents gave rise to a late autumn cohort of young. Throughout the autumn, winter, and spring, grid L had densities that were 1/3–2/5 that on the control.

FIG. 2. (a) Minimum number alive on the control grid and on two experimental grids (X and Z) in 1973-74. Non-breeding periods on the control are shaded. (b) Minimum number alive on the control grid and on grid L (grid L was $4/7$ the area of the control grid). The vertical lines indicate removal of animals.

Survival

The calculation of minimum survival rates from one trapping period to the next includes two components, death and emigration, which cannot be separated by the kind of trapping data collected in this study. Since I am primarily interested in the effect of the experimental treatments on survival, I will make comparisons between the control and the experimental grids only. The number of animals surviving and the number disappearing was tallied for each 2-week trapping interval. These values were then summed over the entire season and a mean survival rate was calculated (Table 4). An individual animal had the possibility of being tallied several times within a season if it was caught in a series of 2-week samples. These mean survival rates are therefore sums of samples which are not independent, and strictly speaking no statistical technique is available for comparing these mean survival rates. I have resorted to chi-square analysis for these comparisons in Table 4, but these results should not be viewed as a statistical test but as an approximate indication of the degree of difference between sets of data.

Five points are shown by Table 4.

(1) On all areas subjected to spring reductions the males survived no better than those on the control grid.

(2) After spring reductions females on grid X survived slightly better than those on the control grid (see below) but not on grid L. Females on grid Z, however, had a total survival rate that was 20% higher than that of the females on the control grid.

(3) During the summer of 1973, when densities were similar on the control grid, grid L, and grid X, survival in all classes in both sexes was also similar.

(4) During the autumn increase period, there was a general trend for higher survival

Table 4. *Minimum survival rates per 14 days for M. townsendii. The survival rates of the animals on the control area, grid I, are given in bold face type; sample sizes in parentheses*

Grid	Adult	Males Young	Total	Adult	Females Young	Total
Spring 1973						
I	0.77 (110)	0.70 (10)	0.77 (120)	0.83 (93)	0.85 (165)	0.85 (258)
L	0.75 (29)	0.44 (6)	0.70 (35)	0.93 (15)	0.77 (31)	0.83 (46)
X	0.70 (49)	0.89 (9)	0.75 (58)	0.88 (23)	0.90 (57)	0.89 (80)
Summer 1973						
I	0.77 (222)	0.49 (39)	0.73 (261)	0.84 (326)	0.69 (65)	0.82 (391)
L	0.73 (93)	0.59 (29)	0.70 (125)	0.81 (105)	0.78 (49)	0.80 (154)
X	0.77 (262)	0.61 (57)	0.75 (319)	0.81 (314)	0.85 (81)	0.81 (395)
Autumn-Winter 1973						
I	0.86 (337)	0.74 (97)	0.83 (434)	0.87 (365)	0.85 (149)	0.86 (514)
L	0.89 (16)	0.93** (53)	0.92 (73)	0.92 (38)	0.85 (50)	0.88 (88)
X	0.91 (127)	0.89* (92)	0.90* (219)	0.87 (71)	0.95* (112)	0.92 (183)
Winter-Spring 1974						
I	0.71 (363)	0.79 (108)	0.72 (471)	0.76 (197)	0.76 (310)	0.76 (507)
L	0.85* (73)	0.96* (25)	0.88** (98)	0.98** (43)	0.94** (67)	0.95** (110)
X	0.94** (117)	0.71 (31)	0.89** (148)	0.88 (75)	0.89* (54)	0.88** (129)
Spring 1974						
I	0.58 (89)	0.00 (2)	0.57 (91)	0.74 (86)	0.62 (32)	0.71 (118)
Z	0.55 (22)	0.67 (3)	0.56 (25)	0.90 (20)	0.92 (12)	0.91* (32)

* $P < 0.05$ for null hypothesis of no difference from control. ** $P < 0.01$.

rates on grids L and X, which had reduced density (significant only in young males on L and X, in the total male sample on X, and in the young females on X).

(5) During the decline period in the winter and early spring 1974, survival in all sex and age groups was consistently 12–23% higher on grids L and X except among the young males on grid X.

Figure 3 show the standardized minimum survival rates for males and females. Standardization was done by measuring the deviation of the experimental rates from the control for each time period. Boonstra (1976) gives the original data on minimum survival rates per 14 days during 1973–4. Poor survival is arbitrarily defined to be any rate below 0.707 per 2 weeks (half or more of the population disappears every 4 weeks). In the spring of 1973, the survival rates of males on grids L and X fluctuated greatly when compared with that on the control. This was caused in part by the small sample size. For example, by the beginning of April, there were only three males left on X and four on L. Survival was nevertheless very poor in certain weeks—five out of nine adult males present on Grid X in mid-March disappeared within the next 2 weeks. During the summer, males on all grids generally showed similar survival rates, with that of males on grid L fluctuating much more than those on the other two grids. These poor survival rates coincided with a drop in density on grid L (Fig. 2(b)). During the autumn and winter of 1973–4, when densities were consistently lower on grids L and X, male survival was almost always better than that on the control. From midwinter to spring, survival of animals on the control grid fell

FIG. 3. Differences in minimum survival rates per 14 days between the experimental grids and the control grid. Minimum survival rates on the control are standardized to a base line of zero. (a) Males; (b) females.

drastically, a drop associated with a sharp decline in densities (Fig. 2). Survival of animals on grids L and X also fell, although it continued to remain higher than that on the control. However, the two age groups were affected differently on grid X. Breeding began approximately 1 month earlier on grid X than on the control grid, so that young of the year were already entering the population well before the end of the decline period. It was these young that were experiencing the poor survival, not the overwintered adults as on the control. For example, at the beginning of April, the twelve young on grid X had a minimum survival rate of 0.5 per 14 days compared with a rate of 0.87 for fifteen adult males on grid X and of 0.42 for nineteen adult males on the control grid. On grid L adults were responsible for the 10% drop in survival rate. On grid Z it was also the adults that were surviving poorly.

In females (Fig. 3), the differences in minimum survival rate between grids were less marked. During the 1973 spring decline, only twenty-six animals (fourteen males and twelve females) were taken from grid X at the first removal, leaving a moderate density on this grid. Survival from this trapping session to the next was not improved over that on the control grid. However, after the next trapping, when all but twenty of the trappable animals were removed and only nine females remained, not one female disappeared during the next 1½ months. This suggests that severe reduction did have a pronounced influence on female survival. Females on grid Z responded in a similar manner during the spring decline of 1974, unlike the females introduced to grid L in 1973. This may have been related to the fact that the latter females were not residents on the area as were the females on grids X and Z.

During the period from May to September 1973, when densities were similar on all areas, survival of females was generally good, but varied sporadically. During the autumn and winter of 1973–4, while densities were kept lower on grids L and X, females on these grids generally survived better than those on the control grid, although not as consistently well as the males. A drop in female survival that occurred on grid X in early April did not occur on grid L, but it corresponded to a similar drop on the control. On both the control and grid X, this poor survival was found in adults, but may have been related to the earlier onset of breeding in grid X females than in either of the female populations on the control grid or grid L.

There is no relationship between density and survival during the spring decline of 1974 in either males ($r = 0.03$, $n = 16$) or females ($r = -0.18$, $n = 16$). During the period included in the analysis (February to mid-April), males on all areas were comparable in breeding condition, but females were lactating 1½ months earlier on grid X than on the control grid, which may have obscured any relationship between density and survival. There was also no correlation between density and survival in the spring of 1973 in males on grids I and X ($r = 0.04$, $n = 12$), but in females the correlation was good ($r = -0.64$, $n = 12$, $P < 0.05$). Data from grid L were not included in this latter analysis because the grid L population was made up of introduced animals, not residents as on grids I and X. I conclude that factors other than density were influencing male survival during the spring decline. In females a negative relationship between density and survival is suggested.

In conclusion, cropping an unmanipulated population while a decline was already in progress had no effect on male survival but did improve female survival. Transferring individuals from a declining area to an evacuated habitat improved neither male nor female survival. Producing low density overwintering populations prior to a decline resulted in improved survival of both males and females both in the autumn and winter.

The higher survival rates of animals on grid X than those on the control grid during the

autumn and winter of 1973–4 could be associated with differences in age structure. In the autumn, all adults had been removed from the grid X population while they were still present in the control population. To see if the differences in survival were real, I grouped the survivorship data for all young caught on the control grid and on grid X during September and October 1973 at a common origin, and used a life table calculation for expectation of further life given by Leslie *et al.* (1955). Figure 4 shows that the calculation for expectation of life of young males on grid X was 7 weeks longer than for young males

FIG. 4. Survivorship curves for males (a) and females (b) first trapped as young in September and October 1973. The vertical lines on the curves represent either removal or accidental death. E_x is the expectation of life (± 1 S.E.).

on control grid I, and in females it was 4 weeks longer. During the first 12 weeks, males on both areas survived well (minimum survival per 2 weeks was 0.93 on the control and 0.92 on X), whereas in the next 12 weeks males on X continued to survive well (0.98) while those on the control survived poorly (0.67). This coincided with the onset of breeding on the control. Females on the two grids showed the same trend, although the differences were less marked (0.93 per 2 weeks on the control and 0.92 on grid X in the first 12 weeks; 0.81 on the control and 0.92 on grid X in the next 16 weeks). Similar calculations were not made for grid L because few young had been recruited by October. In conclusion, the increased survival on grid X compared with that on the control during the autumn and winter of 1973–4 was a real phenomenon, not a consequence of its age structure.

Movements

The low male survival rate observed on the experimental grids after cropping during the decline, may still be related to behavioural interactions. It is possible that after the majority of males were removed from grid X in 1973 and from grid Z in 1974, the remaining males moved over a greater area, thereby keeping the interaction rate constant. An index of movement is the change in position of capture from one trapping period to the next (first capture point in one period to the first capture point in the next). Only movements of adults on the control grid, grid X, and grid Z were compared because the irregular shape of grid L made difficult the comparison of movement. Although movements of both sexes did increase on grid X in the spring of 1973 and on grid Z in the spring of 1974 compared with those on the control grid (Table 5), the differences were not significant. The only significant differences were in the summer, when females moved less on grid X than on the control, and in the fall and winter, when both males and females on grid X moved more. Thus in these latter periods, a decrease in density increased movement, but did not lower survival (Table 4).

Movements within a single trapping period were also examined. An animal could, on first capture, be caught at or near the same location every trapping period but be moving about a great deal within the trapping session. Caution is needed in interpretation of these

Table 5. *Mean distance between successive positions of capture in feet for adults, along with 95% confidence limits. Distances were measured from first capture point of trapping period t to first capture point of trapping period t + 1*

	Males			Females		
	$\bar{x}$	N	95% c.l.	$\bar{x}$	N	95% c.l.
Spring 1973						
Control	30.7	111	24.6–36.8	30.2	87	22.1–38.3
Grid X	39.8	38	26.0–53.5	39.9	21	24.2–55.5
Summer 1973						
Control	35.2	170	30.6–39.7	28.7	270	24.8–32.6
Grid X	35.1	199	30.5–39.6	23.9	233	19.9–27.9
Autumn 1973						
Control	20.5	279	18.0–23.0	19.8	310	17.4–22.1
Grid X	34.6	114	28.1–41.1	31.7	64	23.5–39.9
Winter 1974						
Control	30.7	258	26.6–34.8	25.6	150	21.6–29.5
Grid X	42.3	110	36.0–48.6	47.1	66	38.3–55.9
Spring 1974						
Control	47.4	52	35.1–59.6	32.9	64	27.1–38.7
Grid Z	68.9	12	43.8–94.0	43.7	17	29.4–58.1

data because they may be greatly affected by population density in relation to trap number and trap response of individuals. Similar results to that obtained above for movements between trapping periods were obtained, with both sexes moving about more on grid X during the autumn and winter of 1972 than on the control. However, in 1973–74, there were significant differences between the control grid and grid Z in both sexes. Males on the control moved an average of 31.4 ± 2.3 (1 S.E.) ft compared with 59.5 ± 9.5 ft on grid Z, and females on the control moved 26.7 ± 2.0 ft compared with 51.6 ± 7.3 ft. This suggests that at least in 1974 on grid Z, increased movement was associated with a drastic reduction in population size. However, this suggests, but does not establish, that the interaction rate may have remained high on the low density grid.

DISCUSSION

Drastic reduction in numbers of an already declining population of *Microtus townsendii* did not improve the survival of males, but did improve that of females (Fig. 3). These results suggest that at least in males, survival rates are predetermined and not altered by short term density manipulations. Chitty (1967) suggested that behavioural interactions between aggressive individuals were necessary for a population decline. Do these experiments negate Chitty's suggestion?

The first question we must answer is whether the two decline periods observed (spring 1973 and spring 1974) on the control grid were similar to 'typical' microtine declines. If so, were the causes of these declines the same? The literature indicates that the decline phase is very variable. Chitty (1955) recognized three types of decline: in type M declines, the population fails to overwinter, dropping in numbers after a peak summer; in type G declines, the population overwinters, but steadily decreases throughout the breeding season; and in type H declines, the population declines moderately over the winter after a peak phase, recovers during the following breeding season, and reaches its greatest scarcity the following year. Krebs & Myers (1974), in their review of population cycles, found types H and G about equally common in the literature, and type M declines more rare. The fundamental assumption by Chitty (1967) was that the causal mechanism for these declines was the same.

The two decline periods I observed suggested a type H decline. LeDuc & Krebs (1975) reported that the grid I control population appeared to be going through a more or less typical microtine cycle, with the population increasing rapidly in the fall of 1971, winter breeding occurring during the winter of 1971–2, high numbers being maintained in the summer of 1972 together with heavier body weights, and a spring decline in 1973. The population then recovered rapidly and declined again in spring 1974. However, unlike the type H decline, where lower density is reached in the second year than in the first, numbers fell no lower than in 1973. This suggests that there may be some demographic differences between this species and those reported by Krebs & Myers (1974). In fact, in one of the *M. townsendii* populations that has been studied for 5 years (Krebs *et al.* 1976; C. J. Krebs, personal communication) no major declines were evident. The two declines observed in this study had rates of spring loss that were as high as or higher than those in most of the declines reported by Krebs & Myers (1974). These data, together with those collected by LeDuc & Krebs (1975), suggest that these declines are a local modification of the phenomenon we want to explain.

Many species of microtines have spring declines similar to but shorter than the typical cyclic decline. Spring declines often precede a peak year (Thompson 1955; Chitty & Chitty

1962; Krebs 1964; Krebs, Keller & Tamarin 1969; Gaines & Krebs 1971); though in *M. townsendii* similar declines appear to be unrelated to the peak (Krebs *et al.* 1976). Spring declines are found in other rodent species which have annual cycles in population size (Sadleir 1965; Flowerdew 1974; Fairbairn 1976). These declines are thought to be associated with an increase in aggressive behaviour at the onset of breeding activity. The typical microtine decline may just be a more severe version of the spring decline. I assume that this is the case, and that the declines I observed should be suitable periods for testing a hypothesis about behaviour.

Voies in declining populations do not seem to be experiencing any serious pathological condition. When members of declining populations of *M. agrestis* (L.) and *M. californicus* (Peale) were brought into the lab, survival was normal (Newson & Chitty 1962; Krebs 1966). This is what suggested to Newson & Chitty (1962) that the poor survival in declines was associated with behavioural interactions. However, studies by Chitty & Phipps (1966), Myers & Krebs (1971) and Krebs *et al.* (1976) have found that decline periods are not associated with high rates of dispersal into vacant habitats. In the present study, no individuals were known to disperse during the 1973 decline. Grid G (Fig. 1), a grid separated from grid L by only a 3 m road, experienced the same decline as the control (LeDuc & Krebs 1975) yet no animals that disappeared from grid G were ever caught on L, a low density area. In the 1974 decline, only three animals out of 359 animals disappearing from all grids were known to have dispersed from one grid to another. Therefore, behavioural interactions, if they are occurring, must be severe enough to cause *in situ* mortality. In only one of the studies reported by Krebs & Myers (1974) was wounding judged to be severe enough to cause death. None of the subsequent studies which have looked at wounding have indicated that wounding was ever mortal (Lidicker 1973; Rose & Gaines 1976; R. K. Rose, personal communication). We are left with only two possibilities. Either the animals are making long-range dispersal movements such that they are not attracted to vacant habitat nearby, or some factor which may be related to a type of behaviour not resulting in intensive wounding is causing *in situ* death. Hilborn & Krebs (1976), using a radioactive tagging technique, found a large amount of *in situ* death in one decline and little in another, suggesting that long-range dispersal was a possibility. These results are ambiguous and thus the fate of animals during a decline remains unexplained.

During the spring of 1973, females introduced on to grid L survived at rates similar to those on the control, whereas those on grid X survived much better, as did those on grid Z in the following year (Table 4 and Fig. 3). However, in the latter two cases these females were resident on the areas on which they had overwintered, whereas in the first case this was not so. This may account for their poor survival. These results suggest that familiarity with a site may confer survival advantages to females at low densities. I was also not completely successful in creating a vacant habitat on grid L before the introduction, for I caught eighteen untagged animals 1 week after the introduction.

The social organization of microtine rodents is poorly understood. There is little evidence for the type of territorial behaviour seen in birds (Watson & Jenkins 1968; Krebs 1971; Jenkins, Murray & Hall 1975) but voles are almost equally faithful to their home ranges. To attempt to explain the results obtained in the present study, I propose the following general model of vole behaviour. Adult males and adult females compete for different objects. During the breeding season, females are competing for space in terms of nest sites and large enough areas to promote growth and survival of their young. Their main competitors are therefore other females. Females may also be aggressive to males

and young during the period they are pregnant or lactating (Rowley & Christian 1976). Males, on the other hand, are primarily interested in obtaining females with which to mate. Their main competitors are therefore other breeding males.

The consequences of aggressive interactions may be dependent not so much on density as on the phase of the cycle or perhaps in our local situation, the time of the year. It is possible that environmental factors such as reduced amounts of food and cover, such as in spring before the grass has started to grow, may modify the intensity of the intraspecific competition (Chitty 1952). During the decline, when density is relatively low, these interactions result in disappearance and presumably death, whereas in the increase and peak phases disappearance may more commonly be associated with dispersal (Myers & Krebs 1971). During the non-breeding season, survival should be generally high for both sexes. Most of the mortality occurring at that time should be due to such agents as predation, disease, and environmental stresses, so that both sexes would be affected in a similar fashion and survival in good habitats should be high.

If females are competing for areas in which to raise young, removal of the majority of adjacent females should result in increased survival; this did happen in this study. Removing males from unmanipulated populations at the onset of breeding had no effect on survival, whereas keeping numbers down throughout the winter did improve survival (Fig. 5). It is possible that the overwintering low density populations had set up some sort of relatively stable social structure so that the onset of the breeding season did not result in serious mortality. On the other hand, removing animals from an unmanipulated population might have resulted in a serious disruption of social structure, so that some males might be left on home ranges without females and have to move either from the grid or within it to look for them.

Movements of adult males have been found to be larger than those of females only during the breeding season (Krebs 1966), and home ranges of males are consistently larger (Getz 1961; Ambrose 1969; Van Vleck 1969; Brooks & Banks 1971). Through the use of radio-tracking, Brooks & Banks (1971) were able to follow movements of breeding collared lemmings. They found that adult males had home ranges averaging 2.03 ha compared with only 0.16 ha in females. The males moved about their home ranges continually, visiting each female within it every 1 or 2 days. Similar high rates of activity were found in male brown lemmings (Banks, Brooks & Schnell 1975), and they postulate that the reason for the movement of males is to ensure that they are present when the females are in oestrus, thus increasing their mating opportunities. This may indeed be a general phenomenon in all microtines, with males seeking females and in the process encountering other males.

Few studies have examined behaviour in microtines, and none has done so in the field. Turner & Iverson (1973) found that overwintered adult males were more aggressive, had larger home ranges, and survived longer than young of the year. This suggests that becoming sexually mature in an established population may be extremely hazardous until the overwintered animals have died or been forced out. At high densities, movements and home range of both sexes are less (Getz 1961; Krebs 1966). Krebs (1970) found that aggressive behaviour was higher in peak populations than in increasing populations, which suggests why movements are restricted.

There are still a number of problems with this model. There is no evidence for dispersal during decline periods such as I suggest may occur. Therefore social intolerances in the decline must either lead to mortality without movement or movement is of a long-range nature. A second problem is to explain severe declines from which there is little or no

Population declines in *Microtus*

FIG. 5. Schematic diagram of the changes in survival resulting from reduction of a *M. townsendii* population during (a) and before (b) a decline.

immediate recovery. Lagerspetz (1969) found that in house mice aggression towards another male significantly decreases the sexual behaviour of an inexperienced male mouse towards a female in heat. This decrease in sexual response was partially due to aggressive behaviour towards the female. If there is a change in levels of aggression over the cycle resulting from either a phenotypic or genotypic change in the animals, perhaps the animals become so aggressive as to be unable to mate successfully, or if mating is successful, the young are destroyed. Aggressive behaviour in females, which has received very little attention (Conley 1976), may be critical for survival of the young (Boonstra 1976).

The present study suggests several areas that should be explored further. A greater understanding of social structure and of the interactions that go on in a microtine population is needed. Direct observation of small enclosed populations should be carried out to observe interactions among adult males, adult females, and young, and how these change as a function of reproductive condition and phase of the cycle. In a field population, a combination of intensive live-trapping and of monitoring a fairly large number of individuals by radio-tracking would allow one to form a much more dynamic

picture of the interactions between individuals, the cause of these interactions, and their results. The use of an electrical trapping system similar to that designed by Harling (1971) would permit detection of an animal as soon as it was captured and thus it need not be removed from the population for as great a length of time as is now the case. Radio-tracking of small mammals is currently receiving increasing attention (Brooks & Banks 1971; Chute *et al.* 1974; Banks *et al.* 1975) and appears to be a feasible method for studying microtines in the field. A population expected to experience a decline should be enclosed to see if dispersal is important at this time. Finally, to test the idea that adult breeding males are more interested in obtaining females to mate with than in remaining on a home range, one could remove most of the females from an actively breeding population. The prediction is that the number of adult males remaining on the grid would drop almost at once. An increase in interaction between the remaining males might also occur so that wounding rates might increase.

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SUMMARY

(1) To test part of Chitty's hypothesis (1967) that behavioural interactions are responsible for population declines in voles, I predicted that a drastic reduction in population size during a decline should increase survival.

(2) One control grid was monitored throughout this study and the populations on it experienced severe spring declines in 1973 and 1974.

(3) Three experimental areas were set up; two in early 1973 (X, L) and one in early 1974 (Z). Producing low densities on two of the experimental areas (X, Z) during the spring decline improved the survival of females but not of males. Transferring individuals from a declining population to an evacuated area (L) improved neither male nor female survival. Producing low density overwintering populations (X, L) improved the survival of both sexes.

(4) There was no relationship between density and survival in males in decline periods; in females, there was a negative relationship between density and survival in one decline, but not another.

(5) Relatively more young animals survived the spring decline on a grid maintained at low density (X) than on the control grid.

(6) During the declines, movements of both males and females on the low density areas increased, but only on the grid reduced in the autumn was this significant.

(7) A behavioural model is proposed in which females compete for sites in which to raise young while males compete for females. Cropping experiments to test this model are suggested.

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