A fencing experiment on a high-density population of *Microtus townsendii*

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If dispersal is prevented, a low-density vole population will increase to unusually high densities. A mouse-proof fence was constructed around a vole population that had already reached high density and both this population and one on a control area were live-trapped from January 1975 to November 1975. The population on the control remained at peak densities. The enclosed population increased to even higher density once the breeding season had started and had a higher survival rate than the control population. By midsummer the enclosed population had severely overgrazed the vegetation and went into a sharp decline. Dispersal losses from the control were estimated at 32% for males and 31% for females in these high-density populations. *Microtus townsendii* populations thus responded to a fence in a manner similar to that of other species that have been studied. This experiment indicates the importance of dispersal to population regulation in voles even at peak densities.

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Lorsqu'on empêche la dispersion, chez une population de campagnols de faible densité, cette population atteint bientôt une densité extraordinairement élevée. On a élevé une clôture à l'épreuve des souris autour d'une population de campagnols à densité déjà élevée; une population-témoin a également été étudiée de janvier 1975 à novembre 1975. La population-témoin est restée à sa densité maximale. La population captive a atteint des densités encore plus élevées après le début de la saison de reproduction et le taux de survie de cette population est resté plus élevé que celui de la population-témoin. Au milieu de l'été, la population captive avait épuisé la végétation et a subi une brusque chute de densité. Les pertes dues à la dispersion, dans la population-témoin, s'élevaient à 32% de mâles et 31% de femelles, chiffres rattachés aux populations de hautes densités. Les populations de *Microtus townsendii* réagissent donc à la présence d'une clôture de la même façon que d'autres espèces déjà étudiées. L'expérience démontre l'importance de la dispersion dans le contrôle des populations de campagnols, même lorsqu'elles sont à leur densité maximale.

[Traduit par le journal]

Introduction

Dispersal is an important demographic parameter in rodent populations (Howard 1960; Anderson 1970; Krebs and Myers 1974; Lidicker 1975), and may be critical to population regulation in voles. Dispersal keeps densities well below the level set by the food supply (Krebs *et al.* 1969) and may change the quality of the residents, because the dispersers can differ from the residents both behaviorally and genetically (Myers and Krebs 1971). The amount of dispersal appears to be directly proportional to the rate of population growth (Myers and Krebs 1971; Krebs *et al.* 1976), with animals leaving the population during increase and peak periods. However, dispersal has not been implicated as a cause for decline periods (Chitty and Phipps 1966; Myers and Krebs 1971; Hilborn and Krebs 1976). The voles in the decline must, therefore, be either dying *in situ* or dispersing without settling in nearby vacant habitat.

One way to test the role of dispersal in small rodents is to frustrate dispersal by fencing a population (Lidicker 1975). All fencing experiments done to date were performed on low-density populations, and we need to study the effects of frustrating dispersal in high-density and in declining populations. In this study we fenced a high-density population of *Microtus townsendii* to study the importance of dispersal during the period of high numbers.

Methods

This study was carried out on Westham Island in the delta of the Fraser River near Vancouver, British Columbia. The study area is a pastureland used by the Department of National Defence for communication towers.

The area has had a grass cover since 1946, and has not been grazed since 1963. It is generally flat, with some low-lying areas which are flooded for periods in the winter.

The live-trapping grid used as the control was grid I, which served the same purpose in the experiment of LeDuc and Krebs (1975). This grid has been trapped continuously since July 1971. We set up an enclosure on January 16, 1975, about 60 m from grid I and trapped it until November 12, 1975 (Fig. 1). We used 6.3-mm (¼-in.) mesh hardware cloth extending at least 0.3 m into the ground and 0.6 m above the ground, and enclosing an area of 0.30 h.

The enclosure was bordered on one side by the removal grid, on the second side by a grass strip and a water-filled ditch, on the third side by source area 1, and on a fourth side by a grass–willow strip and another water-filled ditch. The water-filled ditches were effective in impeding movement across them and thus funneling animals escaping from the enclosure to either the removal area or to source area 1. An indication of the effectiveness of these ditches in deterring movement comes from data obtained from the control grid which was separated from the removal grid by about 30 m and a ditch; of the 1468 animals known to have disappeared from the control grid from January to November, only 8 were recaptured on the removal area.

A total of eight areas were trapped on which escapees from the enclosure could have been captured (Fig. 1). All grids were trapped for 2 days every 2 weeks. The control grid was trapped with both livetraps and, during the summer, pitfall traps which captured large numbers of young and transient adults (Boonstra 1976). Grid G was operated throughout the present study to mid-August as part of a food-supplementation experiment. The intact and female grids were operated from March to November; all males were removed from the female grid from May onwards and no animals were removed from the intact grid. The experimental area was operated as a removal grid throughout the spring and summer. Source area 1 was trapped with livetraps and pitfall traps at 2-week intervals from April to June, and thereafter at 6-week intervals; all pregnant females and young were removed each trapping session. Source area 2 was trapped at 6-week intervals with pitfall traps from July to September; only young animals were removed. The removal grid was trapped throughout this study with all animals, except for a small group of young, being removed every trapping session. A total of 1413 animals were removed from this grid during the course of the study, which indicates that this area was a highly effective sink for immigrants. Because of these arrangements we believe we were able to pick up most of the animals escaping from the enclosure.

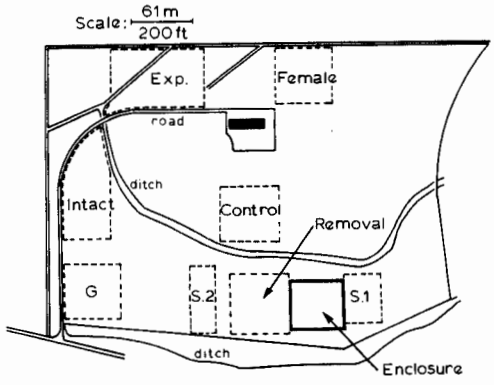

FIG. 1. Map of the study area on Westham Island. S.1 and S.2 were source areas 1 and 2 respectively. Exp. was an experimental grid maintained mainly as a removal area. See text for a description of these areas.

The enclosure was apparently escape proof until June 11, when the first tagged animal was captured on the removal grid. The voles then started tunneling underneath the fence, since the water table had dropped enough to allow deep burrowing. We tried to eliminate as much of this as we could by tamping gravel along the fence edges, but were not completely successful. No voles were known to have climbed over the top of the fence. After June 11, 41 animals are known to have escaped from the enclosure out of the 629 animals caught inside it. All escapees were caught only on the removal area or on source area 1. Seventy-three percent of these animals were caught within 4 weeks after escaping from the enclosure which indicates that most of these animals were very trappable. Another indication that few animals escaped from the enclosure was the nonrandom distribution of the escapees' last position of capture in the enclosure. Over 80% of these animals came from one sector of the enclosure where extensive tunneling underneath the fence was evident ($\chi^2 = 17.8$, $p < 0.001$). From this evidence we conclude that few animals escaped from the enclosure and, of those that did, most were detected.

The control grid was covered by a checkerboard of trap points spaced 7.6 m (25 ft) apart, in a 10 × 10 pattern. The enclosure was about half the size of the control, with traps arranged in a seven by seven pattern. Because of the cost in building the enclosure and the limited area available to put a grid of this nature, we decided that a grid half the size of a normal grid would be suitable. Throughout this study the control was trapped with 150 Longworth livetraps, with two traps at every other trap point. The enclosure was trapped with 74 traps in a similar manner till the end of June, when we added 24 more traps, so that each trap point had two traps. We tried as much as possible to provide an excess of traps. Traps were baited with oats; cotton stuffing was provided. The traps were set every 2nd week on Monday afternoon, checked Tuesday morning, Tuesday afternoon, and Wednesday morning, when they were locked open and left in place. During most of the summer, high temperatures restricted trapping to nights only.

All voles were ear-tagged, and the trap location, sex, sexual condition, and weight of each animal were recorded. Animals escaping from the enclosure were not replaced. In this paper animals are classified as adult (≥43 g), subadult (30 to 42 g), or juvenile (<30 g).

Results

Trappability

Since it is not possible to sample *Microtus* populations randomly, we resorted to the complete enumeration of the trappable population by intensive live-trapping (Krebs 1966 and subsequent

papers). This technique assumes that most of the trappable population is caught each session. Trappability was calculated with the method of Hilborn *et al.* (1976).

The data were separated into three distinct breeding periods. The first period, from now on referred to as the spring, consisted of the main breeding season, which lasted from the beginning of the study to the end of June. The second period, the summer, in which little breeding occurred, lasted from the beginning of July to mid-September. The last period, the fall, in which some voles resumed breeding activity, lasted from mid-September to mid-November.

During the spring, trappability was moderately high on the control, being 74% in males and 62% in females. In the summer, it was low (50%) in both males and females. In the fall, it increased to 62% for males but females showed no marked improvement. Trappability was 10–20% higher in the enclosure than on the control grid, with the difference being most marked in the fall. The higher trappability in the enclosure during the fall was probably due to the lower density in the enclosure relative to the control grid, so that there were more voles per trap on the control than in the enclosure.

Population Density

The trappable population on the control declined only slightly in the spring of 1975 (Fig. 2), averaging 1.6% per week from 17 February to 28 May. The control maintained a high density of over 250 animals for the entire study. The spring decline was sustained almost entirely by the male population, which declined at a rate of 4.1% per week compared with a rate of decline of females of 0.04% per week. The population then increased throughout the summer (2.2% per week) to reach a peak in mid-September of 366 animals. The male population also accounted for most of this increase, which was 4.9% per week compared with 0.5% per week for females. From mid-September to the end of October the population again declined slightly (3.6% per week), owing to a decline in both male and female numbers, with males contributing more to the decline. The correlation between changes in numbers in the total population with the change in male numbers was much higher ($r = 0.86$, $n = 17$, $P < 0.001$) than with the change in female numbers ($r = 0.65$, $n = 17$, $P < 0.01$), indicating that males were the main factor in overall density changes.

To compare the changes that took place in numbers in the enclosure with those on the control, we have corrected for the difference in size between the two areas. To include those animals living on the periphery of the control, we assumed its area included an outer edge equal to the distance between two adjacent trapping points (7.6 m) on the three edges contiguous with grassland and 3.8 m on the edge abutting the ditch.

Most of the overwintering animals in the enclosure had entered the trappable population by April. Figure 2 indicates that the trappable population at this time was higher than that of the control by about 60–80 animals. Part of this difference may be related to overestimation of the correction factor, but it probably represents a real trend because of the higher survival rates of the voles in the enclosure (see below). From the end of June to the beginning of August, the population in the enclosure underwent a period of rapid increase averaging 5.3% per week compared with 3.5% per week on the control. It reached a density 1.4 times that of the control. This very high density of voles severely overgrazed the grass in the enclosure (Fig. 3) so that about three-quarters of the area was completely denuded of all green grass, only a shallow layer of dried grass stems being left. On the control, patches of grass also showed heavy grazing, although nothing comparable with that in the enclosure. From August to mid-October, the population in the enclosure declined at an average rate of 6.4% per week. In the latter part of August, with the onset of the autumn rains, grass started growing again. The population continued to decline at a lesser rate. In mid-October the population started increasing again, after breeding had been in progress for about 1 month.

The 'fence effect' (Krebs *et al.* 1969) was thus evident in this peak population, and resulted in severe overgrazing within a single season after the erection of the enclosure. The correlation between the changes in total numbers in the population with changes in male numbers ($r = 0.81$, $n = 17$, $P < 0.001$) was only slightly lower than with changes in female numbers ($r = 0.87$, $n = 17$, $P < 0.001$), indicating that changes in both were responsible for overall density changes.

Survival

Very few juveniles were caught in the livetraps during this study; most animals on both grids

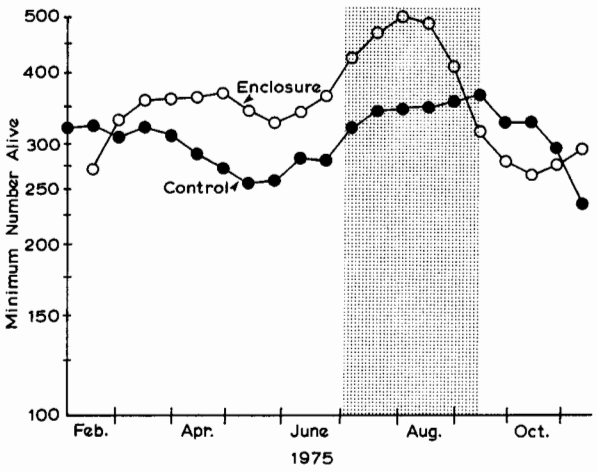

FIG. 2. Minimum number alive on the control grid and on the enclosure. Number on the enclosure was corrected for area by dividing by 0.44. The summer nonbreeding period is shaded.

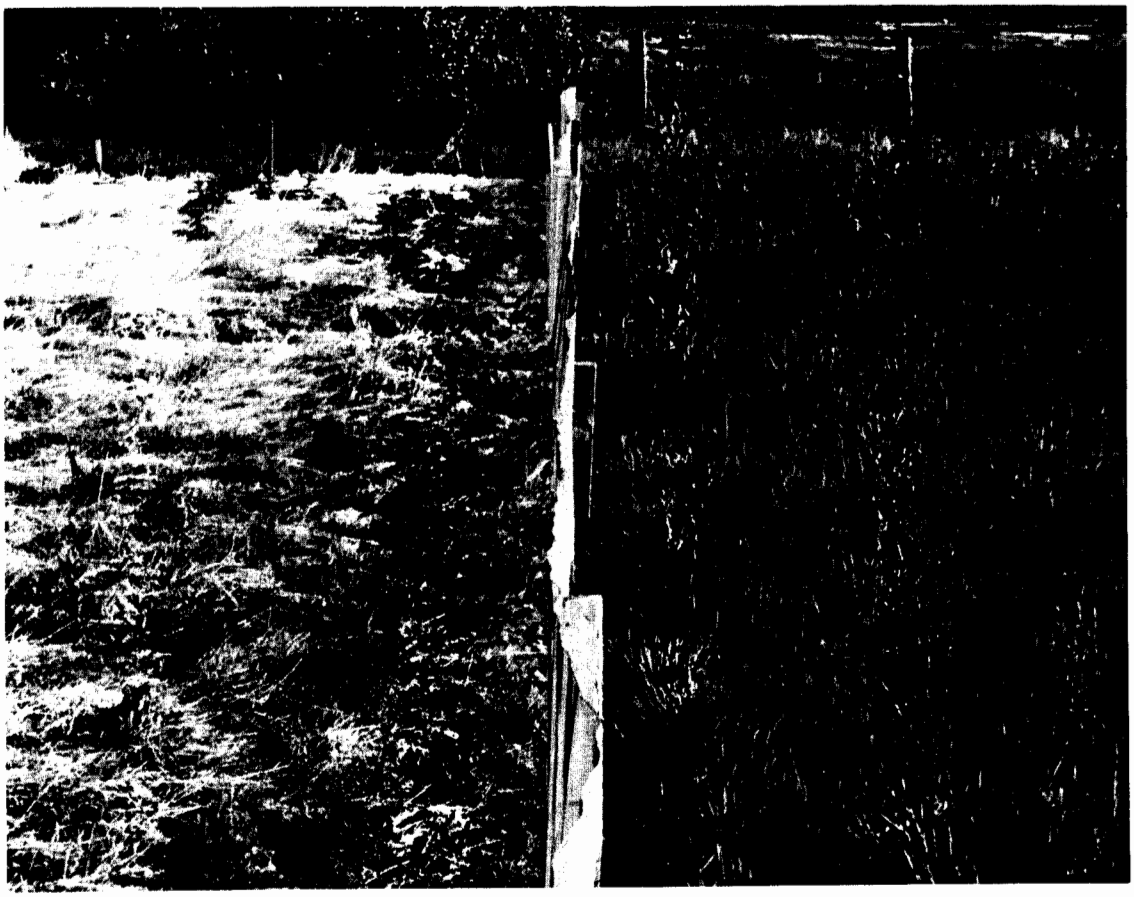

FIG. 3. Photograph of the boundary between the enclosure on the left and a removal grid on the right, July 1975.

entered the populations as either subadults or adults, and we will therefore be referring mainly to these classes. The survival rates presented in Fig. 4 indicate only that animals have disappeared from the trappable population. Disappearance on the control can have been either through death or emigration, whereas disappearance in the enclosure can have been through death only, except for a few animals escaping after June 11. Survival rates of animals in the enclosure were corrected to account for known escapees. To compare the mean survival rates between the enclosure and the control, we have used chi-square analysis.

During the spring, animals on the control survived very well, in contrast with previous years, in which periods of poor survival were recorded (LeDuc and Krebs 1975; Boonstra 1976). Adult females had a survival rate of 0.90 per 2 weeks which was significantly better (by 7–10%) than both adult males and subadult females. During the summer both males and females did poorly, so that over half the population was disappearing every 28 days. These poor survival rates are characteristic of *M. townsendii* every summer, and are associated with the presence of botflies (*Cuterebra* spp.) and grey flesh flies (*Wolhfahrtia vigil* Walker) (manuscripts in preparation). However, Iverson and Turner (1968) report that botflies had no effect on survival in *Microtus pennsylvanicus*. Survival increased slightly in the fall, but did not attain the spring levels. Over the entire study adult females had a survival rate of 0.82 per 2 weeks which was significantly better than adult males and subadult females (by 7% in both cases).

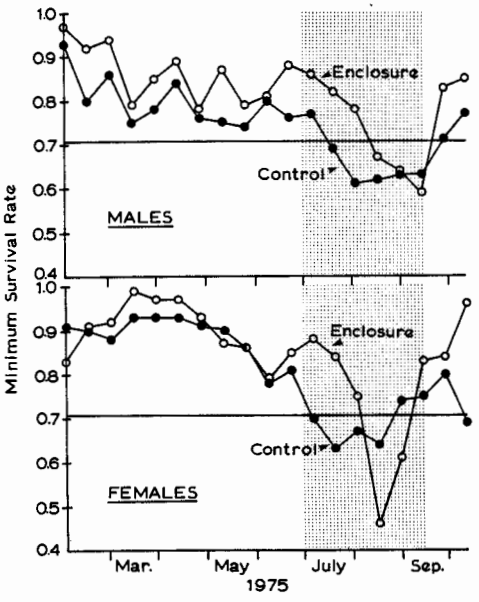

FIG. 4. Mean minimum survival rates per 14 days. The horizontal line is drawn at 0.707, below which half the population disappears every 4 weeks.

Animals in the enclosure generally survived better than did animals on the control. This difference was most pronounced in adult males which had an average survival rate that was 7% better in the enclosure. During the spring and the summer, adult females survived only slightly better, whereas in the fall their survival rates were significantly higher (16% per 2 weeks) than those on the control. In subadult males and females there were no consistent differences in survival rates. Correlation between male and female survival rates in the enclosure was fair ($r = 0.57$, $n = 19$, $P < 0.01$). Correlation between the survival rates of males in the enclosure and males on the control was good ($r = 0.87$), $n = 19$, $P < 0.001$), while correlation between the survival rates of females in the enclosure and on the control was fair ($r = 0.60$, $n = 19$, $P < 0.01$). These correlations indicate that the overall patterns of loss were similar, even though emigration was not possible (for the most part) from the enclosure. This suggests that agents of loss causing *in situ* mortality were acting at similar intensities in both populations.

Although animals generally survived better in the enclosure than on the control, there was a period of about 1 month from mid-August to mid-September when survival in the enclosure dropped drastically (Fig. 3). Females in the enclosure had a mean survival rate of only 0.53 per 2 weeks compared with 0.69 for females on the control ($\chi^2 = 10.2$, $P < 0.005$). Males on the two areas showed no significant differences in survival rates at this time (enclosure = 0.65; control = 0.62), whereas the survival of males in the enclosure had been consistently higher. Part of the poor survival in the enclosure was probably due to starvation and desiccation, since most of the enclosure had neither green grass nor cover. Part was due to escape from the enclosure. The correlation between the number of animals disappearing from the enclosure once the first escapee had been detected in mid-June and the number subsequently caught on the adjacent removal areas was good ($r = 0.72$, $n =$

TABLE 1. Mean reproductive rates for adults on the control and in the enclosure. Data are the proportion of individuals falling into each category summed over the entire period. Sample sizes are in parentheses

Period	Males scrotal				Females lactating			
	Control		Enclosure		Control		Enclosure	
Feb. – June	0.79	(928)	0.85*	(511)	0.35	(1298)	0.32	(670)
July – Sept. 15	0.18	(509)	0.15	(298)	0.02	(482)	0.01	(301)
Sept. 29 – Nov.	0.56	(410)	0.82**	(174)	0.18	(426)	0.42**	(225)

*$P < 0.01$ for null hypothesis of no difference with control.
**$P < 0.001$.

11, $P < 0.05$). However, of the 302 animals disappearing from the enclosure from mid-June onwards, only 41 were captured outside the enclosure. For reasons stated in the methods, we believe that this figure represents the majority of the animals actually escaping. We conclude that animals in the enclosure had a higher survival rate than those on the control during most of the study because of the absence of loss owing to dispersal from the enclosure.

Reproduction

To compare differences in reproduction between the two areas, we used the position of the testes for males and the size of nipples for females. No subadults ever exhibited signs of reproduction, so that this discussion is limited to adults.

Breeding occurred in the spring and the fall of 1975, with very little in midsummer (Table 1). Most adult males (80%) had scrotal testes by the beginning of March, but a large proportion of females was not lactating until mid-April. At the end of the spring breeding period, the number breeding declined more abruptly in females than in males. In the summer, almost no females were lactating, while some males (5–20%) remained scrotal. Breeding in the fall was much less intense than in the spring, with at most 20% of the females lactating and 75% of the males having scrotal testes in a trapping session. Although trapping did not continue until breeding stopped, the percentage of reproductive adults was tapering off more rapidly than it had in the spring.

Reproductive rates in the enclosure were very similar to those on the control. The correlation between the reproductive rates of each of the sexes in the enclosure with those on the control was high (males $r = 0.90$, $n = 21$; and females $r = 0.80$, $n = 21$). Chi-square analyses were performed to test for differences between the two grids. To obtain the sample sizes over an entire period, an animal was tallied into its respective breeding class each time it was captured. There were only two periods in which significant differences between the two grids occurred. In the spring, a greater number of adult males were scrotal in the enclosure than on the control. This appeared to be due to a slightly earlier onset of breeding in the animals in the enclosure. In the fall, both males and females had significantly higher rates of reproduction in the enclosure than on the control. This was associated with lower densities in the enclosure after the decline in the late summer, and with there being a greater quantity of green grass visible in the enclosure. In summary, voles in the enclosure had similar rates of reproduction to those on the control, except in the fall when the rates were much higher in the enclosure.

To obtain a measure of the production per pregnancy, we calculated an index of survival of the young which has been used in other studies on *Microtus* (Krebs 1966, and subsequent papers). This index was the number of new young trapped (<40 g) per lactating female over the entire study excluding the fall breeding period. On the control this index was 0.39 young per lactating female ($n = 457$ females) compared with 0.49 in the enclosure ($n = 220$). These indices were similar and very low. Many young were known to be avoiding traps until they reached adult weight (Boonstra 1976). Little or no immigration into the enclosure probably occurred because of its position between two removal grids and a water-filled ditch. For this reason it is possible to get an index of total production, because all new recruits (adults included) had to be born on the area. Over 50% of the new recruits in the enclosure entered traps as adults. If we assume that immigration and emigration are equal on the control, a comparable figure for total production can be obtained. On the control this

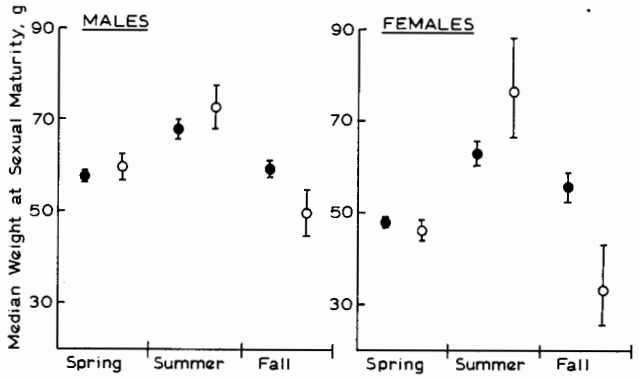

FIG. 5. Median body weight at sexual maturity in animals from the control (●), and the enclosure (○), along with 95% confidence limits.

index was 1.77 recruits per lactating female compared with 1.65 in the enclosure. The slightly higher index on the control may have been due to immigration. Nevertheless, these estimates are roughly equivalent.

Sexual Maturity

The differences in density and reproduction between the two areas can be influenced by differences in the age at sexual maturity. Since the age of voles is not known, weight is used as an index of age. The weight at sexual maturity for live-trapped voles was calculated by the use of the technique of Leslie *et al.* (1945). Maturity in males was judged by the presence of scrotal testes. Maturity in females was judged by the presence of a perforate vaginal orifice, or of medium- to large-size nipples, or of an open pubic symphsis, or of a litter in the trap.

Figure 5 shows that in males, only large animals were mature in the summer, and in females, the high weights at sexual maturity indicate that almost none were becoming mature. In the spring and fall, weights at sexual maturity were 10–40 g less in both sexes for both areas. There are no differences in weight at sexual maturity between the control and the enclosure in the spring breeding period. In the summer, females in the enclosure attained sexual maturity at a significantly higher body weight than did females on the control. However, there were no differences in the percentages of lactating females at this time (Table 1), so that the difference in weight at sexual maturity represented no real difference in reproductive output. In the fall, both males and females matured at significantly lower body weights in the enclosure than on the control. This difference was reflected in a much larger percentage of lactating females in the enclosure. The significant differences between the control and the enclosure coincided with a lower density and more grass in the enclosure.

Discussion

The ability to predict the pattern of population change in voles over a short time period (6 months) presents a good opportunity to test hypotheses of population processes. The object of the present experiment was to prevent dispersal to find out if its absence would change the dynamics of a high density population of *Microtus*. The year 1975 had the highest densities of *M. townsendii* we have ever witnessed.

There were two obvious differences between the winter of 1974–1975 and previous winters. One was the almost complete absence of the seasonal migration of aerial predators. Very few short-eared owls (*Asio flammeus*), rough-legged hawks (*Buteo lagopus*), marsh hawks (*Circus cyaneus*), and snowy owls (*Nyctea scandiaca*) were present. However, great blue herons (*Ardea herodus*) were still observed hunting in the fields, and barn owls (*Tyto alba*) were known to inhabit the local farm buildings. Even the presence of the seasonal migratory predators in other years, however, failed to account for more than a small portion of the total number of voles that disappeared (Boonstra 1976).

The second difference was that the animals were unusually heavy in the winter and spring of 1975. For example, during the first trapping week in February 1975 males on the control grid had an average body weight of 63.7 ± 11.1 g (n =

109) compared with 53.3 ± 9.4 g (n = 63) during the same month in 1974. Females showed a similar 10-g difference between the 2 years. High body weights are characteristic of peak populations in microtines (Krebs and Myers 1974) and are associated with higher growth rates in increasing and peak populations (Krebs *et al.* 1969). The high body weights in 1975 suggest that there was something fundamentally different between the population in that year and those in previous years.

The second reason for this study was to see if *M. townsendii* responded to a fence in a manner similar to other vole species showing strongly cyclic characteristics (Krebs *et al.* 1969). Some of the *M. townsendii* populations studied near Vancouver have shown a number of the characteristics associated with microtine cycles such as winter breeding in the increase period, a shortened summer breeding season in the year of high density, and no breeding in the winter after a peak year (LeDuc and Krebs 1975). However, other populations have shown a gradual increase in numbers over a 5-year period with no marked decline (Krebs *et al.* 1976; Krebs, personal communication). In the declines observed in this species, numbers have never dropped below 44 animals per hectare before increasing again. Therefore, this species does not function in a typical cyclic fashion in this area.

Similar demographic responses to confinement have been found in a number of rodent species by other workers (Strecker and Emlen 1953; Strecker 1954; Clarke 1955; van Wijngaarden 1960; Houlihan 1963). However, these studies are difficult to interpret because the enclosures were very small relative to the size of the home ranges of the animals, the animals were maintained on artificial food, and predation was absent. Only two studies have examined the effect of enclosing field populations of microtines (Gentry 1968; Krebs *et al.* 1969). In Gentry's experiment there was a great deal of movement between the two enclosures and presumably also out of them. Only in the experiment of Krebs *et al.* were the enclosures relatively escape proof and thus comparable with this study. They found the following characteristics in *M. pennsylvanicus* and *M. ochrogaster* populations when these were enclosed in a fence: (1) higher rates of population increase in the increase and peak periods on the fenced areas than on the unfenced areas; (2) much higher densities on the fenced areas; (3) higher survival rates in the fenced populations; and (4) severe overgrazing of the vegetation, resulting in a decline through starvation. The enclosed population in our study exhibited all of these characteristics.

Since the population in this study was at peak numbers when it was enclosed, severe overgrazing occurred within 6½ months of the erection of the fence. In the two species studied by Krebs *et al.* (1969), the populations started at low densities and took 13–17 months before overgrazing the habitat.

The evidence presented in Boonstra (1976), where livetraps and pitfall traps were used, indicates that the actual number of voles on the control during the summer of 1975 was more than twice the number enumerated by Longworth livetraps. A small number of pitfall traps put out near the end of the spring breeding period in the enclosure also indicated that a large segment of the population temporarily avoided capture in livetraps. Of the 104 animals first caught in pitfalls, 36 failed to enter livetraps subsequently. This evidence together with that of severe overgrazing and higher survival rates within the enclosure suggests that there were over 519 animals per acre (1281 per hectare) in the enclosure, which was the maximum number enumerated on the control. This compares with a maximum of 200 animals per acre in *M. ochrogaster* (494 per hectare) in an enclosure in Indiana where only livetraps were used (Krebs *et al.* 1969).

This study again indicates the importance of dispersal in keeping *Microtus* densities below the limit set by the food supply. Dispersal from peak populations of *M. pennsylvanicus* was found to account for 33% of the losses of males from control areas and 25% of the losses of females (Myers and Krebs 1971). These workers found that dispersal was related to the onset of breeding condition, and that more males dispersed than females. This higher dispersal rate in males corresponded to the lower apparent survival rate of this sex. An estimate of the fraction of the losses that were possibly due to dispersal can be obtained in the present study if one assumes that the difference in survival between the enclosed and control populations in each trapping session was due to emigration from the control, and that the rest was due to *in situ* mortality on both areas. Only the period from February to July was examined, because after this time the number of animals escaping from the enclosure in-

creased sharply, and survival fell drastically because of overgrazing. This estimate indicates that dispersal accounted for 32% of the losses in males and 31% of the losses in females. These figures are comparable with those found by Myers and Krebs (1971). Since very few adult voles disappearing from the control grid were ever caught again on other trapping areas (Boonstra 1976), the animals that did disperse must either have moved only short distances before suffering high mortality rates, or must have moved long distances before settling down. The cause of this dispersal is unknown, but is presumed to involve some form of aggressive behavior. This aggressive behavior is not sufficient to cause death if dispersal is eliminated as evidenced by the increased survival in the enclosure. What actually kills dispersers is unknown, but may involve selective predation on an animal unfamiliar with an area through which it is moving (Metzgar 1967) or failure to find a nest site.

The high reproductive rates exhibited in the enclosed population in the fall (Table 1) may have been the result of two factors. First, the population in the enclosure had just suffered a severe decline and was at lower density compared with that on the control. Characteristically, microtines in the peak phase have a shortened breeding season that may be inversely related to density (Kalela 1957; Zedja 1967). However, similar shortened breeding seasons have been found at low densities such as in decline years (Krebs 1964). This suggests that in typical cyclic microtines shortened breeding seasons may not be related to density per se but to the phase of the microtine cycle. *Microtus townsendii* appears to be somewhat atypical with regard to demography, so that it does respond to reduced density by breeding more intensively. Secondly, there was a large flush of green grass that was more evident in the enclosure during this period. Negus and Pinter (1966) suggest that vegetation in the early growth stages may stimulate reproductive processes through estrogenic-like substances in the plants. However, the onset of the breeding season may be delayed even in the presence of growing vegetation or continued into the dry season (Krebs 1966). Therefore the exact cause of the differences in breeding rates is unknown.

Krebs *et al.* (1973) postulated that differential dispersal of certain genetic and behavioral groups of animals observed during the phase of increase caused the quality of the voles remaining at peak densities in wild populations to be different from the quality of voles in enclosures, where no selection through emigration could occur. Exactly what causes vole populations to decline remains a puzzle. An experiment, similar to the one we performed here, on a population experiencing a decline, would help to explain how and why animals disappear. An alternative experiment would be to provide a dispersal sink (a vacant habitat from which animals are removed) (Lidicker 1975) for a fenced population and follow this population through a cycle. This would allow dispersers to be identified, and to determine when dispersal occurs.

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