# *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*

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If spacing behavior limits the breeding density of small mammals, the colonization of vacant areas by surplus animals ought to show how and when population regulation is achieved. Two 0.8-ha areas near Vancouver, British Columbia, were cleared of voles from May 1971 to December 1973 and the colonization of the cleared areas was monitored every 2nd week. All colonists were removed. The colonization rate of the experimental areas was most rapid when populations were increasing rapidly in the adjacent control areas, and much of the loss of individuals in increasing control populations was due to dispersal rather than death. In declining populations very little dispersal occurred. Voles of high body weight (>60 g) were characteristic of late increase and peak populations, but few of these heavy voles dispersed to the vacant experimental areas. Weight at sexual maturity was lower in colonizing voles, particularly among females. About 25% more males than females dispersed into the vacant areas. Colonizing voles were not a genetically random subsample from the control populations. Some leucine aminopeptidase (EC 3.4.11.1) genotypes were more prone to dispersal, particularly when populations were increasing. These results are in agreement with the results of earlier experiments on *Microtus pennsylvanicus* and *M. ochrogaster*, and they point to the need for more detailed studies of the dispersal process in voles.

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S'il est vrai que le comportement d'espacement limite la densité reproductrice des petits mammifères, la colonisation d'aires libres par les animaux de surplus devrait pouvoir démontrer de quelle façon et à quel moment le contrôle de la population se manifeste. On a procédé à une expérience de mai 1971 à décembre 1973: on a évacué les campagnols dans deux aires expérimentales de 0.8 ha, près de Vancouver, Colombie Britannique, et mesuré la recolonisation des aires vidées, toutes les 2 semaines. Tous les colonisateurs étaient ensuite retirés de l'aire. La colonisation des aires expérimentales se fait à un taux plus rapide lorsque les populations des aires témoins adjacentes augmentent rapidement; la perte d'individus dans les populations témoins en croissance est généralement due à la dispersion plutôt qu'à la mortalité. Lorsque les populations subissent une décroissance, il se produit très peu de dispersion. La présence de campagnols de poids lourds (>60 g) est caractéristique des populations en fin de croissance et des populations ayant atteint leur sommet de densité, mais peu de ces campagnols migrent vers les aires expérimentales vacantes. Le poids à la maturité sexuelle est plus bas chez les campagnols colonisateurs, particulièrement chez les femelles. La dispersion dans les aires vides implique environ 25% plus de mâles que de femelles. Les campagnols colonisateurs ne constituent pas, du point de vue génétique, un sous-échantillon aléatoire des populations témoins. Quelques génotypes, caractérisés par la leucine aminopeptidase (EC 3.4.11.1), sont plus enclins à la dispersion, particulièrement lorsque les populations augmentent. Ces résultats corroborent ceux d'expériences antérieures sur *Microtus pennsylvanicus* et *M. ochrogaster* et soulignent l'importance d'investigations plus complètes des procédés de dispersion des campagnols.

[Traduit par le journal]

## Introduction

Many vole and lemming populations fluctuate periodically in size. One way to investigate the causal mechanisms underlying these fluctuations is to stop the fluctuations from occurring. At present the only experimental technique that has been successful in stopping population fluctuations in the field is fencing of an area (Krebs *et al.* 1969). Fencing a small rodent population prevents dispersal, and we believe that the 'fence effect' indicates that dispersal is necessary for normal population regulation in voles.

Dispersal is rarely studied in population work, and we require some operational techniques for measuring dispersal. Myers and Krebs (1971) adopted the trapped-out area as a technique for defining dispersing individuals. An area is maintained free of resident voles by continuously removing animals which colonize it. Myers and Krebs (1971) reached two major conclusions from their study of dispersal in *Microtus pennsylvanicus* and *M. ochrogaster*: (1) dispersal occurred most commonly during the phase of population increase, and few animals dispersed when the population was declining; and (2) dispersal was genetically selective, so that dispersing voles were not a random sample from the surrounding populations. This study was designed to test the generality of these two conclusions in another species, *M. townsendii*, and to describe the demographic attributes of dispersing voles through a periodic fluctuation in numbers.

## Methods

Two replicate areas were set up near Vancouver, British Columbia. Each area consisted of a pair of live-trapping grids, 30 m (100 ft) apart, one a control grid and the other a complete removal grid. The removal areas were purposely situated in the corners of fields, so that in each case no immigration was possible from two directions. Each area was live-trapped for 2 days and nights every 2nd week from May 25, 1971, to December 5, 1973. Each trapping area had 100 trap points spaced 7.6 m (25 ft) apart. Longworth live traps were left in position between trapping periods and locked open so that voles could move freely in and out. When population densities became high, we doubled the number of live traps.

Each individual vole was ear-tagged upon first capture, and its weight, sex, breeding condition, and location on the grid recorded. A blood sample was taken from each animal from the suborbital sinus at the time of first capture. Voles were released immediately after processing on the control grid and removed permanently from the removal grid.

Population parameters were determined by enumeration techniques to avoid the statistical assumptions of random sampling. Hilborn (1974) has demonstrated that enumeration techniques provide accurate estimates for our trapping situation in which 80% or more of the voles are caught each sampling time.

The two areas chosen for replicate experiments turned out not to be as similar to each other as we would have liked. The Serpentine Fen study area (grids C and D) is situated along the south bank of the Serpentine River about 1.5 mi (2.5 km) east of Mud Bay. It contains *Microtus townsendii* almost exclusively. The Ladner Airbase study area (grids E and F) is situated in the southwest corner of an old airport complex, about 100 m from Boundary Bay. It contains a mixed population of *M. townsendii* and *M. oregoni*, and is a drier site than the Serpentine Fen. Both of these areas lie in a matrix of several hundred acres of grassland and are not subject to disturbances from local farming practices.

All voles were characterized genetically at a marker locus controlling the enzyme leucine aminopeptidase (LAP) (EC 3.4.11.1, aminopeptidase (cytosol)). Two alleles have been detected in our populations and these are inherited as if controlled by a simple autosomal locus (LeDuc 1974). Three LAP phenotypes can thus be recognized: LAP-S, LAP-F, and the heterozygote LAP-S/F.

## Observations and Results

### *Weather*

Coastal British Columbia has a mild climate. Winters are mild and wet; summers are warm and dry. Very little snow falls on lowland areas. Temperature extremes are moderated by the ocean. Temperature never reaches highs or lows that are detrimental to voles on our study areas. Heavy winter rains are more of a problem. During the winter the water table is often at ground level and voles cannot usually burrow. There is some variation from year to year in winter rainfall patterns. The winter of 1971–1972 was notable for its snowfall. In December 1971, 31.6 in. (80 cm) of snow fell at the Airport, and snow was on the ground for 15 days. In January 1972 the corresponding figures were 14.1 in. (36 cm) of snow and 10 days. The following winter, 1972–1973, was more typical; 11.1 in. (28 cm) of snow fell and covered the ground for only 9 days in December and January. The fall of 1972 was drier than usual and more sunshine was recorded, especially during October. The spring of 1973 (February to April) was also drier and sunnier than the previous year.

### *Trappability*

All of the demographic analysis to follow is based on the assumption that we are able to catch most of the individuals in these populations. We define trappability as follows:

$$\text{trappability} = \frac{\text{no. actually caught at time } i}{\text{no. known to be present at time } i}.$$

Table 1 gives the trappability estimates for our two control populations. Trappability is always above 70%. There is a lower trappability on grid C than on grid E, and this is associated with a higher density on grid C. There is a suggestion of slightly reduced trappability in the summer months, at least on the more densely populated grid C. Males and females have equal trappability. Note that these estimates of trappability

TABLE 1. Trappability estimates for *Microtus townsendii* on the two control areas. *N* is the sum of the number known alive over the time period. Trappability is the proportion of those known to be alive that are actually caught in a trapping session

| | Grid C | | | | Grid E | | | |
|---|---|---|---|---|---|---|---|---|
| | Males | | Females | | Males | | Females | |
| Time period | $T^a$ | $N^b$ | *T* | *N* | *T* | *N* | *T* | *N* |
| Jun.–Aug. 1971 | 0.70 | 281 | 0.80 | 305 | 0.90 | 50 | 0.79 | 39 |
| Sep.–Nov. | 0.82 | 132 | 0.92 | 150 | 0.97 | 34 | 0.90 | 78 |
| Dec.–Feb. 1972 | 0.81 | 113 | 0.80 | 194 | 0.96 | 51 | 0.74 | 105 |
| Mar –May | 0.98 | 101 | 0.97 | 119 | 0.96 | 45 | 0.81 | 73 |
| Jun.–Aug. | 0.79 | 165 | 0.80 | 197 | 0.86 | 106 | 0.96 | 91 |
| Sep.–Nov. | 0.79 | 202 | 0.88 | 228 | 0.86 | 123 | 0.98 | 137 |
| Dec.–Feb. 1973 | 0.90 | 367 | 0.85 | 396 | 0.90 | 156 | 0.94 | 177 |
| Mar.–May | 0.95 | 255 | 0.93 | 306 | 0.87 | 142 | 0.99 | 130 |
| Jun.–Aug. | 0.75 | 370 | 0.76 | 528 | 0.83 | 203 | 0.81 | 182 |
| Sep.–Nov. | 0.77 | 446 | 0.81 | 598 | 0.83 | 162 | 0.80 | 142 |
| Total | 0.81 | 2432 | 0.83 | 3021 | 0.87 | 1072 | 0.88 | 1154 |

[a] *T* = trappability.
[b] *N* = sample size.

are maximum estimates since there could be some voles which are not caught at all. We know that juveniles and subadults are difficult to trap in *M. townsendii*, but we feel that few adult voles escape being trapped.

*Population Density and Dispersal*

The population changes in *Microtus townsendii* were similar but not identical on the two control areas, and hence we will discuss them separately. Figure 1 shows density changes on control grid C. In May 1971 when the study began, this population was declining rapidly from high density. The decline stopped in the autumn of 1971 and the population remained low during the fall, winter, and spring of 1971–1972. A phase of population growth began in the spring of 1972 and continued on through the winter of 1972–1973, and high numbers were reached in the summer and fall of 1973. This period of increase averaged only 2–3% gain per week. Two short time periods of dropping numbers were superimposed on the general increase trend. Both males and females declined slightly during the summer of 1972 but at different times: males declined May 22 to July 3; females, June 19 to August 28. A second decline of both sexes occurred in the late winter of 1972–1973. From early January until the end of March both sexes lost about one-third of their numbers. Thus the control population on grid C went through a decline, a period of low numbers, and then increased to reach a high density in 1973.

The *Microtus townsendii* population on control grid E (Fig. 2) was at low numbers when this study began in May 1971. A phase of increase began in summer 1971 and continued during the next summer. The winter period of 1971–1972 was characterized by a drop in numbers, but a slight rise in numbers occurred during the next winter of 1972–1973. The population was at moderate density during the summer of 1973. Three short time periods of dropping numbers were superimposed on these general trends. The first drop occurred at the start of the study from June to August 1971, and males were particularly affected. The other two drops were both late winter declines from late January until late March in 1972 and again in 1973. Both sexes were affected by these late winter declines, and in each case about one-third of the population disappeared. Thus the control population on grid E went through a long period of increase, followed by a stationary phase at moderate density. Note that the maximum density on grid E was only one-third that of maximum density on grid C.

The number of *Microtus townsendii* removed from grid D is also given in Fig. 1. Note that all these voles were removed so there is no continuity of population from one trapping period to the next. The colonization rate of this removal

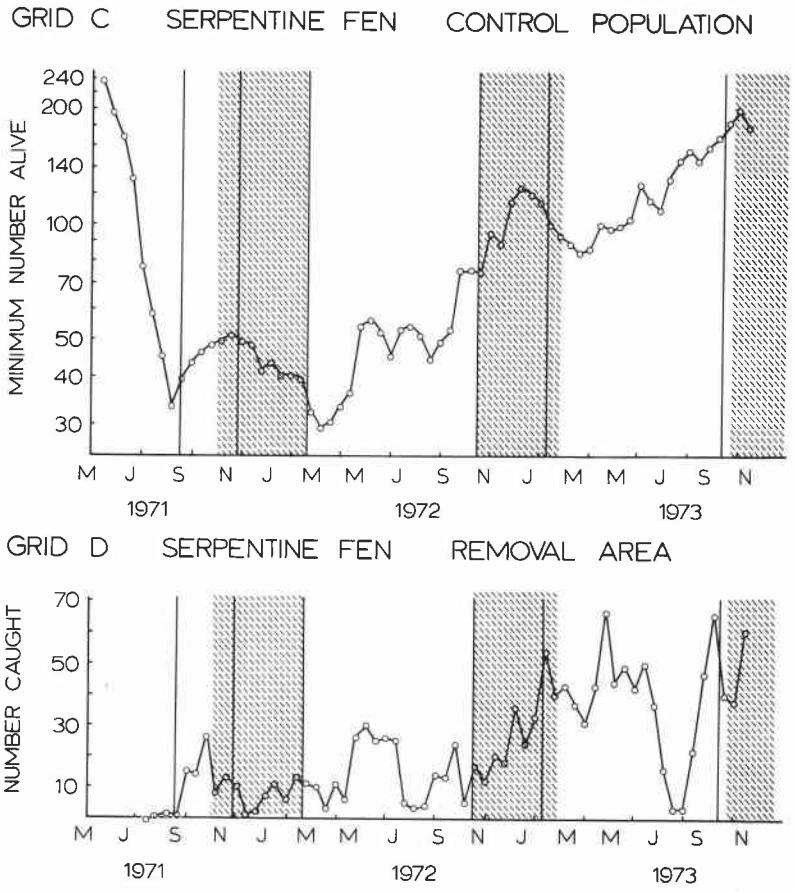


FIG. 1. Population density of *Microtus townsendii* on control grid C and removal grid D at the Serpentine Fen. Winter months are shaded. Vertical lines mark the limits of summer and winter breeding periods. Both sexes are combined. All voles were removed from grid D as they were captured.

grid is highly variable. There was a high immigration rate in midsummer 1972 and an even higher rate in summer of 1973, as the population was approaching high density. There was very little movement into this grid during the latter part of the decline in 1971. Unfortunately we had to spend June and the first half of July of 1971 clearing the removal grid of its residents, so we could not determine the immigration rate during the first part of the decline. During the phase of low numbers in the winter of 1971–1972 there was also little colonization of the removal area. A total of 1310 voles was removed from this grid during the study.

Data from the replicate removal grid F are shown in Fig. 2. The colonization rate of this area is lower than that occurring on grid D. Relatively high immigration occurred in the middle of the summer of 1973, associated with a moderately dense population. A total of 483 voles were removed from grid F during the study.

Dispersal (or colonization) rate can be measured in several ways. Some of the immigrants to the removal grids are tagged voles from the adjacent control population. Hence we can separate marked and unmarked immigrants. We consider four measures of dispersal rate: number of immigrants, number of tagged immigrants, recovery ratio, and recruitment index.

$$\text{Recovery ratio} = \frac{\text{no. voles removed from removal grid at time } i}{\text{population size on control grid at time } i}.$$

$$\text{Relative recruitment index} = \frac{\text{no. voles removed from removal grid at time } i}{\text{no. new recruits tagged on control grid at } i}.$$

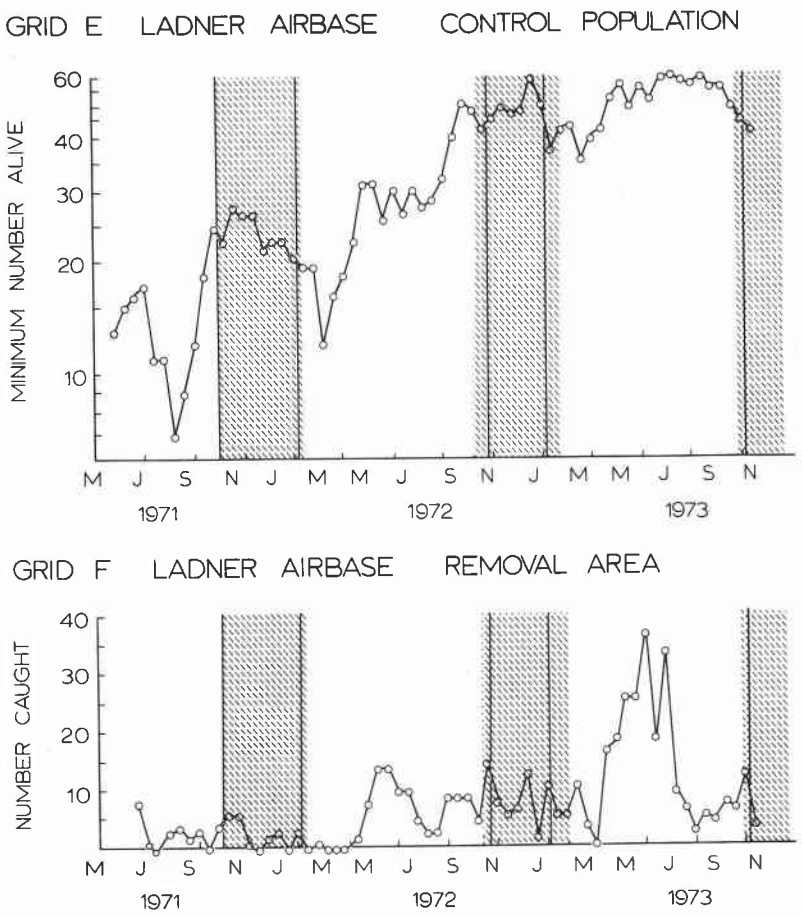


FIG. 2. Population density of *Microtus townsendii* on control grid E and removal grid F at the Ladner Airbase. Winter months are shaded. Both sexes combined.

Table 2 presents these four measures for the experimental populations.

We first ask whether any of these measures of dispersal rate is correlated with either the density of the control population or the rate of population change ($r$) of the control population. To determine this we grouped data into broad periods covering the "summer" and "winter" of each year. The winter period was determined on biological grounds as the time of reduced reproduction. The limits of these time periods are shown by vertical bars in Figs. 1 and 2. The summer and autumn of 1971 had to be broken into two periods for grids C and D because of the population decline during the summer months. Simple correlation coefficients between the density of the control population and the measures of colonization of removal areas are given in Table 3. The most striking correlation is between the density of the control population and the number of immigrants coming into the experimental areas. The number of immigrants is also significantly affected by the rate of population growth of the control. The partial correlation of the number of immigrants with the rate of population growth is 0.76, when the density of the control is held constant. By knowing the density and rate of growth of the control population we can explain statistically 94% of the variation in the number of immigrants moving into a depopulated area.

The number of tagged immigrants is less easily related to events in control populations. It is correlated only with the rate of growth of the control population and not with density of the control. One possible explanation may be that the number of tagged immigrants is too low and therefore subject to chance variation.

TABLE 2. Population density for control populations and colonization data for removal areas, *Microtus townsendii*. All data are mean values for time periods shown in Figs. 1 and 2

| | Average density | Rate of popln. growth[a] | Av. no. immigrants[b] | Av. no. tagged immigrants[b] | Recovery ratio[c] | Relative recruitment index[d] |
|---|---|---|---|---|---|---|
| Grids C and D | | | | | | |
| Summer 1971 | 46.3 | −0.132 | 1.0 | 0.7 | 2.7 | 0.27 |
| Fall 1971 | 47.0 | +0.035 | 13.7 | 3.0 | 28.5 | 1.33 |
| Winter 1971–1972 | 43.9 | −0.016 | 8.1 | 1.6 | 18.9 | 2.08 |
| Summer 1972 | 49.4 | +0.024 | 15.2 | 2.1 | 30.9 | 1.33 |
| Winter 1972–1973 | 105.7 | +0.033 | 23.9 | 2.0 | 22.4 | 1.64 |
| Summer 1973 | 125.8 | +0.016 | 39.6 | 2.4 | 34.6 | 1.98 |
| Grids E and F | | | | | | |
| Summer 1971 | 13.9 | +0.023 | 2.8 | 1.1 | 22.7 | 0.70 |
| Winter 1971–1972 | 23.3 | −0.007 | 2.6 | 0.9 | 11.5 | 0.93 |
| Summer 1972 | 28.8 | +0.026 | 6.2 | 1.6 | 19.2 | 1.02 |
| Winter 1972–1973 | 49.7 | −0.017 | 7.8 | 2.0 | 16.0 | 1.34 |
| Summer 1973 | 50.0 | +0.003 | 13.3 | 1.8 | 25.9 | 1.82 |

[a]Instantaneous rate per week.
[b]Per 2 weeks.
[c]Ratio of the number of voles removed from experimental area divided by population size in control area.
[d]Number of recruits into the experimental area divided by number of recruits captured in control area.

TABLE 3. Correlation coefficients between population density on control grids and four measures of dispersal into the removal areas. Data in Table 2. Both areas were combined in this analysis ($N = 11$)

| Control popln. | Av. no. immigrants | Av. no. tagged immigrants | Recovery ratio | Relative recruitment index |
|---|---|---|---|---|
| Density | 0.93** | 0.50 | 0.45 | 0.57 |
| Rate of popln. growth | 0.42 | 0.61* | 0.79* | 0.49 |

*Significant at 5% level.
**Significant at 1% level.

The recovery ratio is a useful measure of the resiliency of the control population, and could be termed a 'colonization rate.' On the average about 20% recovery could be expected in 2 weeks on the removal area, but this ranged widely from no recovery to 50% recovery. This variation in colonization rate is largely associated with the rate of increase of the control populations, and only slightly associated with the density of the control. About 73% of the variation in the recovery ratio could be associated with the rate of growth and density of control populations.

The relative recruitment index is not clearly related to the changes in control populations. This index averaged 1.31 over the study, which means that the number of colonists on the removal areas was 31% greater than the number of new voles caught on the control area. In spite of a continuous removal which prevented most reproduction *in situ*, more new voles turned up on the removal grids than on the controls.

In summary, the *number* of voles moving into a depopulated area is largely correlated with the density and the rate of population growth in surrounding areas. Colonization of vacant areas is rapid when populations are increasing rapidly in surrounding areas.

*Survival and Dispersal*

Some of the voles tagged in the control areas were later captured and removed from the experimental areas. Some of the loss of individuals from the control can thus be explained, and we now inquire what this fraction is and how it is related to density changes in control populations.

Most tagged individuals which turned up on

TABLE 4. Number of tagged *Microtus townsendii* disappearing from control populations and later removed from experimental areas. Males and females are combined

| | No. tagged voles lost from control | No. tagged voles removed from experimental | % loss explained by dispersal |
|---|---|---|---|
| Grids C and D | | | |
| Summer 1971 | 110 | 4 | 4 |
| Fall 1971 | 53 | 15 | 28 |
| Winter 1971–1972 | 34 | 12 | 35 |
| Summer 1972 | 149 | 38 | 26 |
| Winter 1972–1973 | 67 | 14 | 21 |
| Summer 1973 | 262 | 42 | 16 |
| Grids E and F | | | |
| Summer 1971 | 33 | 11 | 33 |
| Winter 1971–1972 | 23 | 6 | 26 |
| Summer 1972 | 93 | 32 | 34 |
| Winter 1972–1973 | 35 | 11 | 31 |
| Summer 1973 | 139 | 37 | 27 |
| Grand total | 998 | 269 | 27.0 |

the removal areas had only recently left the control area. The average interval between last capture on the control area and capture on the removal area was 2.9 weeks for 155 animals from grid C and 2.6 weeks for 94 animals from grid E. Very few animals disappeared from the control areas more than 6 weeks before appearing on the removal area.

Table 4 gives the number of voles lost from the control populations and the fraction of these which turned up as dispersing animals on the removal area. Of all the known losses from control populations, 27% could be explained by dispersal of tagged voles to the removal areas. The percentage of loss explained by dispersal was positively related to the rate of increase of the control population ($r = 0.65$, $n = 11$, $p < 0.05$) but not related to the density of the control population ($r = -0.46$, not significant). Little of the loss in the declining grid C population during summer 1971 could be explained by dispersal, and the high-density population on this grid in summer 1973 had the next lowest percentage of losses explained by dispersal into the experimental areas.

Survival rates of female *Microtus townsendii* were closely related to the population growth rate of control populations ($r = 0.82$). Male survival rates are only poorly related to population growth rates as described earlier for *M. pennsylvanicus* and *M. ochrogaster* (Krebs 1971). Consequently, the percentage of loss explained by dispersal is also related to female survival rates ($r = 0.78$). This correlation is opposite in sign to what one might expect: the better the survival, the more of the loss that can be explained by dispersal from the control to the removal areas. Loss due to dispersal is thus not density-dependent in *Microtus townsendii*, nor is it delayed density-dependent.

### *Body Weight and Dispersal*

Body weight in voles is partly related to age and is a convenient if crude index to use for determining the age structure of dispersing and resident voles. Dispersing voles can never be a random sample of the entire population because very small juveniles cannot disperse. Our live-trap samples refer to only a part of the population which is sufficiently mobile to encounter traps. Adult *Microtus townsendii* weigh 50–80 g and voles first caught in live traps average 30–40 g (about 6–8 weeks old). We wish to ask first if there are any differences in the average weights of voles recruiting into the experimental population compared with the control population.

Figure 3 shows the body weight distributions of males for the Serpentine control population during this study. There is a considerable amount of seasonal and year-to-year variation in male body weights. During the period of low numbers in late 1971, body weights are particularly low on grid C. No males over 58 g were caught in the winter of 1971–1972, and breeding activity,

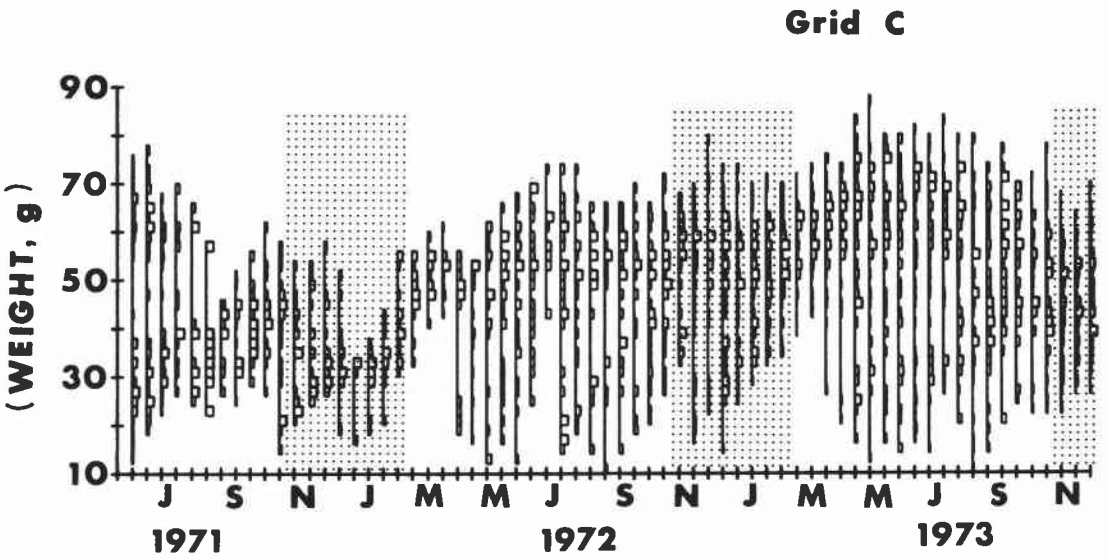


FIG. 3. Body weight distributions for male *Microtus townsendii* from the control population on grid C, Serpentine Fen.

which was at a moderate level in November and December 1971, stopped altogether in January and February 1972. By contrast, breeding continued at a moderate level throughout the winter of 1972–1973 and males up to 78 g were caught in December. Spring and summer weight distributions also differ between years. Average male weight at the start of the summer breeding was 50.2 g in March 1972 and 57.6 g in March 1973. The largest male in March 1972 was 58 g; in 1973, 73 g. Males average 15% larger on grid C in summer 1973 compared with 1972. The same pattern, and an even more striking contrast between years, was found on grid E. Males averaged a full 10 g larger in March 1973 than in March 1972.

Female body weights are complicated by undetected pregnancies and these data are more variable than the data for males presented in Fig. 3. Female weights, however, show all the changes described for the males. In particular, females were 10% larger in summer 1973 compared with summer 1972 on grid C, and on grid E they were 11% larger.

We now inquire whether all size classes of voles colonize the removal areas in the same proportions as they occur in the control population.

The weights of voles colonizing the experimental areas suggest that these individuals are not always a random sample from the control population. Figure 4 shows the mean weights of control and experimental males for the summer and winter periods. Grid D voles were the same size as control grid C voles until summer 1973. In this population at moderate to high density there were fewer large males (>60 g) in the experimental population (Fig. 5). Grid E voles showed the same trend when compared with grid F voles throughout 1972 and 1973. Both these results suggest that individuals of high body weight, which are characteristic of high-density populations, do not disperse into vacant habitat. Colonizing voles in dense populations are smaller than resident animals. These results were found in both males and females.

*Sexual Maturity and Dispersal*

Age at sexual maturity is a critical demographic variable, and we now inquire whether voles which colonize the removal areas are maturing at the same age as control animals. Since we do not know the age of our voles, we must use weight as an index of age. We would expect a priori that growth rate of individuals would be equal or better on the removal areas, and thus equal-aged voles might be slightly heavier in the experimental populations.

We estimated the weight at sexual maturity for live-trapped voles in the way described by Leslie *et al.* (1945). Maturity in males was

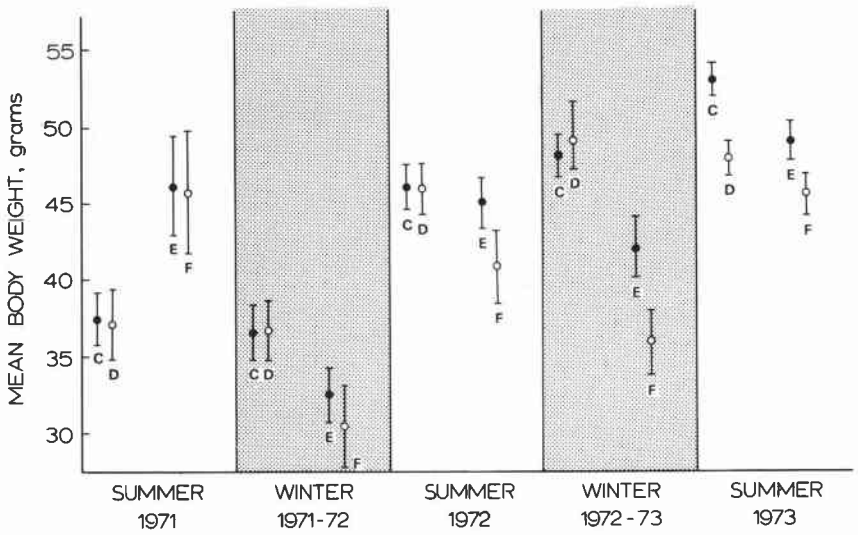


FIG. 4. Mean body weights of male *Microtus townsendii* from control populations (C, E) and their paired experimental populations (D, F). Data are grouped over the summer and winter periods indicated in Figs. 1 and 2. Vertical bars give 95% confidence limits.

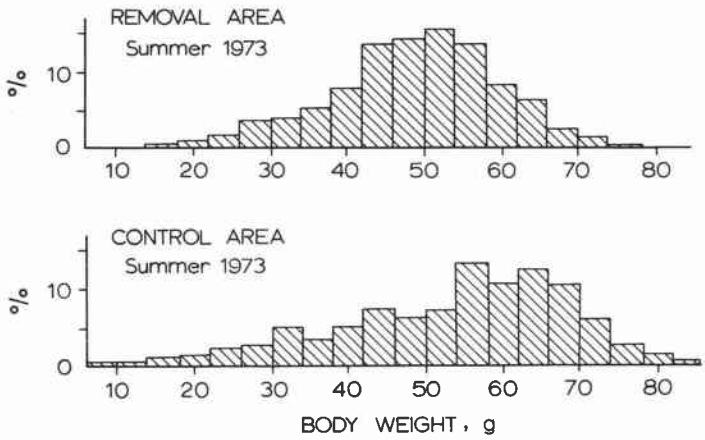


FIG. 5. Body weight distributions for male *Microtus townsendii* from control grid C ($n$ = 733) and experimental grid D ($n$ = 376) during the summer of 1973. Few voles above 60 g colonize the removal area.

judged by the presence of large testes. This is a crude index, but by periodic reference to voles later autopsied we have tried to keep this judgement relatively accurate. Female maturity was judged by the presence of a perforate vaginal orifice, or medium- to large-size mammary glands, or open pubic symphyses, or a litter in the live trap. We feel the judgement of female maturity is more accurate than that of male maturity. There is probably a bias in our female data, however. Females in the early part of their first pregnancy will often show none of the external signs listed above, and without an autopsy we classify them as non-breeding. There is no reason to expect this bias to differ between experimental and control populations. Data for 3-month periods were grouped to determine the percentage mature in 4-g weight classes. A probit line was then fitted to these percentage mature data, as described by Leslie *et al.* (1945).

The weights at sexual maturity for female voles from grids C and D are shown in Fig. 6.

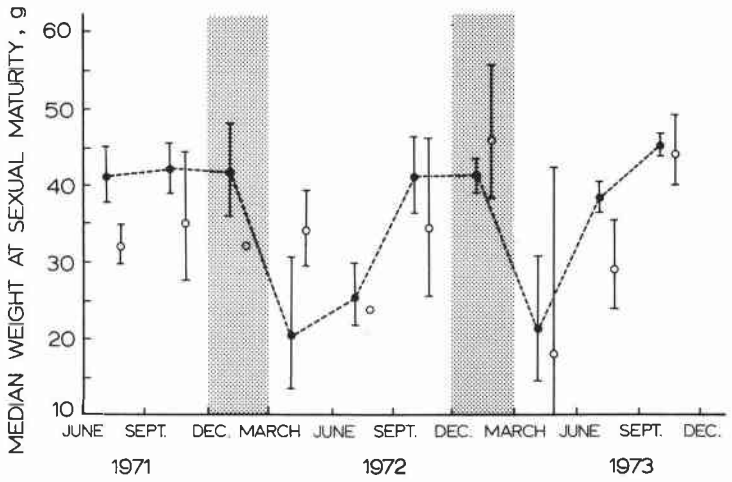


FIG. 6. Median body weight at sexual maturity for female *Microtus townsendii* from control grid C (●) and experimental grid D (○), along with 95% confidence limits. Winter months are shaded.

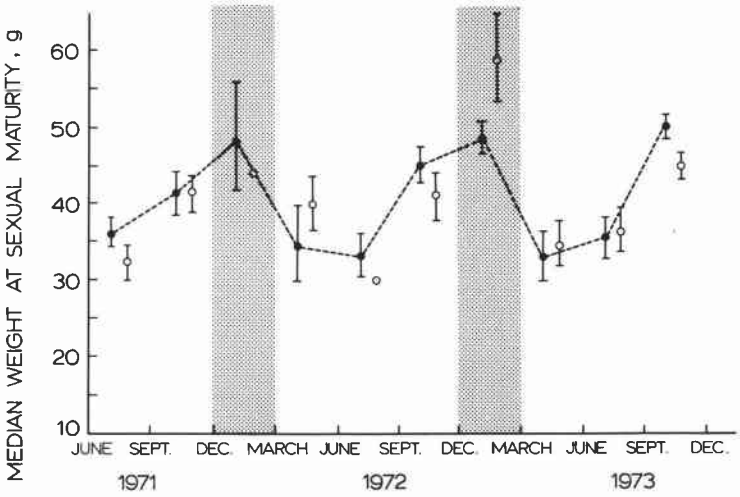


FIG. 7. Median body weight at sexual maturity for male *Microtus townsendii* from control grid C (●) and experimental grid D (○), along with 95% confidence limits. Winter months are shaded.

There is an annual cycle in the average size at sexual maturity in the control population. Only the heavier voles are mature during the fall and winter months. Females from the experimental area tend to mature at lighter weights than do the control females. Few of the individual means are significantly different because of the broad confidence intervals, but in 8 of 10 periods the median weight for the experimental is less than that for the control. Data from grids E and F confirm these trends, and again in 8 of 10 cases the females mature at smaller size on the experimental area. By contrast, males on the experimental areas do not seem to differ in weight at sexual maturity from males on the control areas. Figure 7 gives the male data for grids C and D. The pattern of change resembles that of the females (Fig. 6) in 1971 and 1972. In only 5 of 10 cases do experimental males mature at lighter weights than control males.

Further information on the breeding condition of colonizing voles was obtained by looking at the subadult weight class (30–42 g). Table 5 gives the percentage of subadult males and females that were in breeding condition. There is a tendency for subadult voles from the removal

TABLE 5. Percentage of subadult voles in breeding condition in control and experimental areas. Sample size in parentheses. Comparisons between experimentals and controls that are statistically significant are in italics

| Grid | Summer 1971 | Fall 1971 | Winter 1971–1972 | Summer 1972 | Winter 1972–1973 | Summer 1973 | Total for summers 1971–1973 |
|---|---|---|---|---|---|---|---|
| Males[a] | | | | | | | |
| Grid C | *45.7* | 30.4 | 5.9 | 46.7 | 8.8 | 40.4 | *43.4* |
| | (70) | (46) | (51) | (60) | (68) | (114) | (244) |
| Grid D | *69.4* | 21.4 | 11.1 | 60.0 | 8.7 | 50.0 | *57.2* |
| | (36) | (28) | (27) | (35) | (23) | (74) | (145) |
| Grid E | 80.0 | | 14.3 | *51.1* | 13.2 | 56.5 | *57.1* |
| | (15) | | (35) | (47) | (38) | (92) | (154) |
| Grid F | 75.0 | | 28.6 | *79.3* | 12.5 | 68.6 | *72.8* |
| | (12) | | (7) | (29) | (24) | (51) | (92) |
| Females[b] | | | | | | | |
| Grid C | *24.3* | 25.9 | *34.7* | 50.7 | 31.8 | *40.6* | *42.3* |
| | (37) | (58) | (75) | (136) | (157) | (281) | (454) |
| Grid D | *54.8* | 47.4 | *77.8* | 46.4 | 36.4 | *56.1* | *53.8* |
| | (42) | (19) | (9) | (56) | (33) | (164) | (262) |
| Grid E | 59.5 | | 22.4 | 44.2 | 42.2 | 54.0 | 51.5 |
| | (42) | | (49) | (104) | (90) | (126) | (272) |
| Grid F | 66.7 | | 0.0 | 59.3 | 66.7 | 64.2 | 62.9 |
| | (9) | | (1) | (27) | (6) | (53) | (89) |

[a]Maturity judged by size of testes.
[b]Maturity judged by perforation of vaginal orifice.

TABLE 6. Sex ratios (proportion of males) in control and experimental populations of *Microtus townsendii*. Sample size in parentheses

| | Summer 1971 | Fall 1971 | Winter 1971–1972 | Summer 1972 | Winter 1972–1973 | Summer 1973 | Total for all summers[a] |
|---|---|---|---|---|---|---|---|
| Grid C | 0.44 | 0.44 | 0.37 | 0.45 | 0.49 | 0.42 | 0.43 |
| (control) | (448) | (246) | (246) | (726) | (619) | (1726) | (2698) |
| Grid D | 0.41 | 0.61 | 0.58 | 0.52 | 0.62 | 0.53 | 0.53 |
| (removal) | (270) | (82) | (57) | (258) | (167) | (712) | (1052) |
| Grid E | 0.47 | | 0.37 | 0.46 | 0.44 | 0.52 | 0.50 |
| (control) | (131) | | (158) | (492) | (276) | (853) | (1476) |
| Grid F | 0.63 | | 0.57 | 0.57 | 0.68 | 0.65 | 0.63 |
| (removal) | (54) | | (21) | (117) | (47) | (264) | (435) |

[a]Total for grids C and D includes the fall 1971 period in place of the summer 1971 period, which involved a declining population.

areas to be in breeding condition more often than one would expect from the control population. If we total the data for the summer breeding season, about 10–15% more subadult males and females are in breeding condition on the experimental areas, compared with the controls.

We conclude that voles which colonize the removal areas are breeding at smaller sizes and younger ages than voles on control areas. This difference is particularly well marked in females but is also present in males.

*Sex Ratios of Dispersing Voles*

We next inquire whether voles which colonize the removal areas are predominately one sex. The sex ratio of the control areas was estimated by tallying each animal every time it was trapped and summing these data over seasonal periods. This technique provides a weighted average sex ratio for the resident population.

Table 6 gives the sex ratios for the two sets of control and experimental populations. The results are unambiguous: more males colonize the removal areas than females. The sex ratio is higher on the removal areas in every period except for the summer of 1971 on grids C and D.

There is considerable age variation in the voles colonizing removal areas, and we need to know whether an excess of males occurs in all age classes. Because weight is such a crude index of

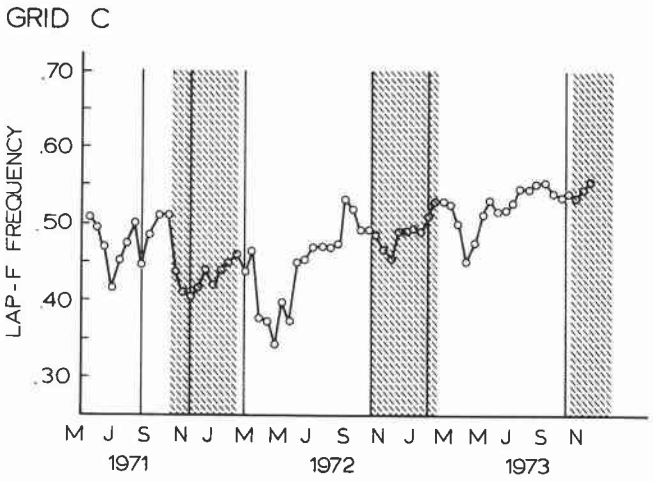


FIG. 8. Gene frequency changes at the LAP locus in the Serpentine control population of *Microtus townsendii*. Winter months (Nov. to Feb.) are shaded. Solid vertical lines separate the winter and summer breeding periods.

age, we have used only two age classes: less than 30 g (juveniles) and 30 g and above. The same picture was obtained on both study areas: no significant difference in sex ratio between juveniles from experimental and control areas and a great excess of males in older voles from the removal grid ($p < 0.01$).

We can also compare the sex ratios of voles from the removal areas with those of new recruits on the control areas. There are more males among new recruits to the control grids, and the sex ratio of new recruits to the control and that of removal area recruits are not significantly different. There is still a slight (2–5%) excess of males on the removal areas but this excess is not statistically significant.

*Genetic Composition*

One polymorphic serum-protein system has been available to us to characterize the genetic composition of resident and dispersing voles. The enzyme leucine aminopeptidase occurs in two electrophoretically distinguishable forms in our populations, a slow (S) band and a fast (F) band. We typed 96% of the individuals on the control area at Ladner, and 86% of the removal animals. At the Serpentine Fen we typed 86% of the controls and 91% of the removals. Our estimates of gene frequencies are thus almost parameter values for our particular local areas.

Figure 8 shows the changes in allele F frequency in the Serpentine control population. LAP-F frequency varied from 35 to 55% over the study. During the population decline and low of 1971 the LAP-F frequency dropped from about 50% to 40%. The population began to increase in 1972 and the gene frequency also increased from 40% to 55%. The long period of increase in LAP-F frequency was punctuated by two periods of reversal. Both reversals occurred at the end of the spring decline in density in April 1972 and again in late March 1973.

Figure 9 shows the changes in LAP allele F frequency in the Ladner control population. Changes in allele frequency are more dramatic in this population, and observed frequencies ranged from 15 to 60% over the 3 years of study. The frequency of LAP-F tended to drop during winter periods and increase during the summer breeding seasons each year. The overall trend is thus for population density increases to be associated with increases in LAP-F frequency.

We wish to inquire whether the voles colonizing the experimental removal areas are a random genetic sample from the resident populations illustrated in Figs. 8 and 9. Tables 7 and 8 give the proportions of the three LAP phenotypes in the control and experimental populations. Data are grouped into the time periods designated by the vertical lines in Figs. 8 and 9. Of the 22 statistical comparisons ($\chi^2$ tests) made in these two tables, 7 are significant, and we conclude that colonizing voles are often not a genetically random subsample of the control population. Fewer signi-

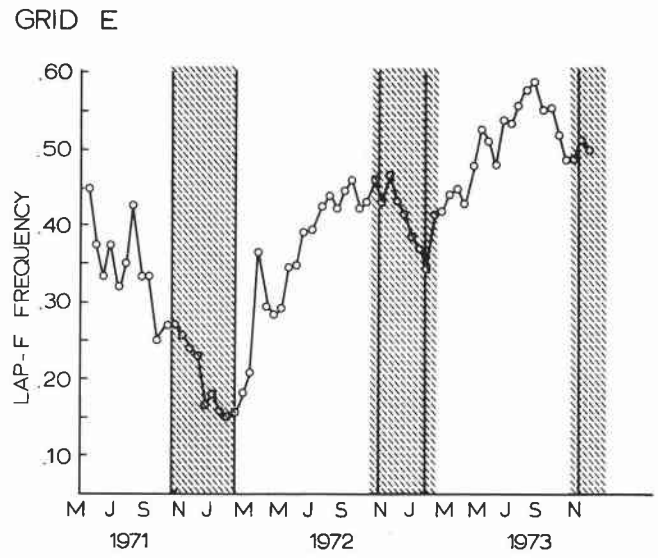


FIG. 9. Gene frequency changes at the LAP locus in the Ladner control population of *Microtus townsendii*. Winter months (Nov. to Feb.) are shaded. Solid vertical lines separate the winter and summer breeding periods.

ficant differences are found in the Serpentine grids C and D than in the Ladner grids E and F. Note that opposite effects are present on the Serpentine and Ladner areas during summer 1972. On Serpentine grid D, the colonizing voles are LAP-F more frequently than expected; on Ladner grid F, LAP-F individuals are rarely caught as colonizers, and there was an excess of heterozygote females among the colonizers during summer 1972. But LAP-F individuals are not always underrepresented on the removal area at Ladner. During the winter of 1971–1972 there was an excess of LAP-F among the colonizing voles of both sexes at Ladner. We do not understand why these differences occur within one area, and can only point to the association of relatively low densities with more LAP-F dispersal and relatively high density with little LAP-F dispersal at the Ladner Airbase.

We have analyzed the observed and expected proportions of heterozygotes among the residents and the colonizing animals. The results add little to what is given above. There is a correlation between the LAP-F and LAP-F/S phenotypes such that a deficiency of LAP-F individuals is always associated with an excess of heterozygotes. Conversely, an excess of LAP-F voles is associated with a deficiency of heterozygotes.

We also compared the genotype frequencies of voles colonizing the removal areas with those of new recruits to the control population. The results of this comparison were basically the same as indicated in Tables 7 and 8 and hence we do not present these comparisons.

## Discussion

In this experiment we attempted to maintain areas free of adult voles, and then to measure the rate of colonization into the vacant area. We identify the individuals which appear on the vacant area as 'dispersers' and we imply that they are surplus individuals, driven out of adjacent populations, and would normally be lost. Several assumptions are critical for this experimental design, and we now consider possible deficiencies in this design.

A major assumption of this experiment is that the removal of voles from the experimental area does not affect population processes on the control area. Voles can move over large home ranges (Harvey and Barbour 1965; Robinson and Falls 1965), and if the removal area is too close to the control area, one could be cropping the resident population of the control. This difficulty would suggest having the removal area a great distance from the control but two problems then arise: (1) one would catch very few tagged individuals

TABLE 7. Proportion of three leucine aminopeptidase (LAP) phenotypes in dispersing and resident populations of *Microtus townsendii* on grids C and D at the Serpentine Fen

| | Summer 1971 | Fall 1971 | Winter 1971–1972 | Summer 1972 | Winter 1972–1973 | Summer 1973 |
|---|---|---|---|---|---|---|
| | | | Males | | | |
| Grid C (control) | | | | | | |
| LAP-F | 0.29 | 0.23 | 0.00 | 0.23 | 0.27 | 0.31 |
| LAP-F/S | 0.41 $n = 210$ | 0.42 $n = 126$ | 0.74 $n = 106$ | 0.42 $n = 368$ | 0.45 $n = 341$ | 0.49 $n = 811$ |
| LAP-S | 0.30 | 0.35 | 0.26 | 0.35 | 0.28 | 0.19 |
| Grid D (removal) | | | ** | | | |
| LAP-F | 0.14 | 0.33 | 0.22 | 0.24 | 0.27 | 0.28 |
| LAP-F/S | 0.56 $n = 70$ | 0.33 $n = 45$ | 0.59 $n = 32$ | 0.46 $n = 127$ | 0.44 $n = 97$ | 0.52 $n = 358$ |
| LAP-S | 0.30 | 0.33 | 0.19 | 0.31 | 0.29 | 0.21 |
| | | | Females | | | |
| Grid C (control) | | | | | | |
| LAP-F | 0.20 | 0.26 | 0.18 | 0.21 | 0.20 | 0.26 |
| LAP-F/S | 0.52 $n = 242$ | 0.46 $n = 146$ | 0.57 $n = 193$ | 0.52 $n = 446$ | 0.55 $n = 379$ | 0.48 $n = 1198$ |
| LAP-S | 0.28 | 0.28 | 0.25 | 0.27 | 0.25 | 0.26 |
| Grid D (removal) | | | | * | | |
| LAP-F | 0.27 | 0.20 | 0.08 | 0.32 | 0.33 | 0.30 |
| LAP-F/S | 0.55 $n = 105$ | 0.44 $n = 25$ | 0.58 $n = 24$ | 0.47 $n = 116$ | 0.44 $n = 61$ | 0.48 $n = 322$ |
| LAP-S | 0.18 | 0.36 | 0.33 | 0.21 | 0.23 | 0.22 |

*$p < 0.05$.
**$p < 0.01$.

TABLE 8. Proportion of three leucine aminopeptidase (LAP) phenotypes in dispersing and resident populations of *Microtus townsendii* on grids E and F at the Ladner Airbase

| | Summer 1971 | Winter 1971–1972 | Summer 1972 | Winter 1972–1973 | Summer 1973 |
|---|---|---|---|---|---|
| | | Males | | | |
| Grid E (control) | | | | | |
| LAP-F | 0.08 | 0.00 | 0.16 | 0.14 | 0.21 |
| LAP-F/S | 0.62 $n = 63$ | 0.45 $n = 60$ | 0.48 $n = 242$ | 0.55 $n = 135$ | 0.56 $n = 527$ |
| LAP-S | 0.30 | 0.55 | 0.36 | 0.31 | 0.23 |
| Grid F (removal) | * | * | | | * |
| LAP-F | 0.33 | 0.12 | 0.17 | 0.11 | 0.11 |
| LAP-F/S | 0.38 $n = 21$ | 0.38 $n = 8$ | 0.46 $n = 48$ | 0.53 $n = 19$ | 0.47 $n = 102$ |
| LAP-S | 0.29 | 0.50 | 0.38 | 0.37 | 0.42 |
| | | Females | | | |
| Grid E (control) | | | | | |
| LAP-F | 0.12 | 0.07 | 0.20 | 0.19 | 0.25 |
| LAP-F/S | 0.33 $n = 81$ | 0.26 $n = 125$ | 0.32 $n = 271$ | 0.47 $n = 157$ | 0.52 $n = 462$ |
| LAP-S | 0.54 | 0.66 | 0.48 | 0.35 | 0.22 |
| Grid F (removal) | | ** | * | | |
| LAP-F | 0.29 | 0.50 | 0.07 | 0.00 | 0.18 |
| LAP-F/S | 0.29 $n = 7$ | 0.50 $n = 6$ | 0.59 $n = 29$ | 0.82 $n = 11$ | 0.56 $n = 68$ |
| LAP-S | 0.43 | 0.00 | 0.34 | 0.18 | 0.26 |

*$p < 0.05$.
**$p < 0.01$.

that disperse from the control; (2) one might question whether the distant control population is an adequate representation of events going on around the removal area.

Interference between the control and removal populations would be suspect if a significant fraction of voles tagged on the control were removed each trapping session on the removal area and if high numbers of voles on the removal area coincided with a drop in density on the control grid. Neither of these conditions was obtained in this study, and we had numerous cases of individuals with constant home ranges on the control grid along the side of the grid closest to the removal area. To check possible interference more rigorously we would have to maintain a 'near' and a 'distant' control grid, or else alternate 2-month periods of removal and nonremoval on the experimental area. We have not been able to do these more rigorous tests.

A second assumption of this experimental design is that we can catch the colonizing voles by trapping only 2 days every 2nd week. There are two conflicting aspects of this problem. We know that *Microtus townsendii* is particularly difficult to live-trap and they will enter live traps quickly only if they have been used previously by other voles. Thus it usually takes a few weeks for individuals to become trappable. It is possible that there is a class of dispersing voles which do not enter live traps easily and which may move on to another area within 2 weeks. An alternate design would be to trap the removal area continuously. Unfortunately, this design would catch and remove individuals from the control area that were making a brief foray of a few hours into adjoining habitats. We have not tried to do a continuous removal in this experiment.

Individuals caught on the removal area are not all dispersers. Some individuals from adjacent areas may be caught making a brief foray into the removal area. A few females no doubt avoided capture long enough to raise a litter in the removal area. We have assumed, however, that most animals we remove are indeed surplus animals colonizing a nearly vacant habitat.

Tagged animals which moved into the removal area were caught and removed very quickly, so we had no evidence in this study of animals moving into the removal area and staying there without getting caught in the live traps. To check our removal efficiency we replaced all the live traps on four occasions with snap traps and continued the removal for one extra day. The normal live-trap removals, with the additional kill-trap catch in parentheses, were: 25 (2), 11 (1), 17 (1), and 15 (0). We thus estimate that we missed only about 6% of the adult voles on the removal areas when we live-trapped. We assume in this calculation that *Microtus townsendii* do not avoid snap traps baited with peanut butter.

A third assumption of this experimental design is that population density on the removal area does not build up fast enough to affect demographic parameters in the 2 weeks between removal. We would like to assume that we are measuring the primary characteristics of dispersing individuals, but in some cases we do not know if this is a valid assumption. For example, subadults may colonize the removal area and because of the low density of voles begin to reach sexual maturity. If our samples show more sexually mature subadults, we do not know whether these animals were maturing as they arrived or only after they arrived on the removal area.

One design to investigate this assumption is to remove voles only in pulses of, for example, 1 month removal, 2 months mark and release. We are currently doing this experiment on *Microtus townsendii*.

We assume in this experiment that voles which colonize the removal areas are surplus animals which are not capable of holding down a breeding area in the surrounding, unmanipulated area (Watson and Moss 1970). One alternative view might be that colonizing voles are just individuals which wander about, shifting homesites every few weeks or months. We require behavioral criteria to distinguish these alternate views. The first view suggests that colonizing voles are socially subordinate animals, but the second view does not make this prediction. In this study we do not have the behavioral data to verify this important assumption. The first view would also predict that most wandering voles are males, since male wanderers are more likely than female wanderers to make a genetic contribution to the next generation.

Only one previous experiment of the type described here has been carried out, that of Myers and Krebs (1971) on *Microtus pennsylvanicus* and *M. ochrogaster*. The most significant conclusion from this previous work was that dispersal was most common from increasing populations and rare from declining populations. We

found a similar result in this study. We considered four different measures of dispersal rate, and found all of them to be positively related to population density and rate of population growth on the control grid (Table 3). We continue to be puzzled by this conclusion. When the control populations are growing most rapidly, they are also apparently exporting the largest number of surplus individuals. We presume this is due to behavioral interactions between individuals in the control populations. What then is occurring during the population decline? Few surplus animals seem to exist in the decline phase, and this might suggest that behavioral interactions are not severe at this time, or alternatively that behavioral interactions have become so severe that they are lethal. Garten and Smith (1974) used a drift fence and pitfall traps to catch all the *Peromyscus polionotus* leaving a population in South Carolina. Their results were an exact replica of ours, and again dispersal was not found during the population decline.

The number of voles recruiting into the removal area continues to amaze us. We removed far more animals from the experimental areas, on which virtually no litters can be produced, than we ever catch on the control areas. The immigration rate into established populations is clearly much less than the immigration rate into vacant areas. Our observations thus satisfy conditions (*a*) and (*b*) of Watson and Moss (1970, p. 170) to show that dominance and spacing behavior limit the breeding density of voles. Similar findings have been reported by Davis *et al.* (1964) on woodchuck populations.

Myers and Krebs (1971) showed that most of the loss of voles from expanding populations could be due to dispersal. We found the same result for *Microtus townsendii*. When survival is excellent, most of the individuals disappearing seem to be dispersing rather than dying. Myers (1974) observed the same effect in feral populations of *Mus musculus*.

The ecological attributes of dispersing individuals are rarely known, and we have tried to describe some of the attributes of individuals which colonized the removal area. We would like to know the age distribution of colonizing animals, but we are unable to age voles and we can only use body weight as a rough index of relative age. A wide size distribution characterizes the voles which enter the removal area. Both males and females usually have the same spread of body weights as control animals, with the single exception that the very large animals characteristic of peak populations did not seem to disperse very often (Fig. 5). Myers and Krebs (1971) found that dispersing females of *Microtus pennsylvanicus* and *M. ochrogaster* were smaller than the control animals, but the same effect did not occur in males of *M. pennsylvanicus*.

Dispersing females of *M. townsendii* reach sexual maturity at smaller sizes than do control females, and we believe this indicates a lower age at sexual maturity. We were not able to show this effect very clearly among the males. Myers (1974) described this effect for dispersing females in house mice. We do not know if sexual maturity develops before dispersal and leads to adverse behavioral interactions and thence dispersal, or whether voles disperse before they become mature and are stimulated to breed by the low-density environment of the removal area. Table 5 shows that breeding was severely restricted on both experimental and control areas during some winters, so that voles colonizing the vacant area in midwinter do not automatically begin to breed because of the low density.

More males than females colonize the removal area, and Myers and Krebs (1971) got the same result. The surprise is that the sex ratio is not even more biased than it is (Table 6). A large fraction of the colonizing voles are females, and dispersal is not a male prerogative. Thus voles differ in degree from marmots, in which dispersal occurs predominately in males (Armitage 1973), and from pikas, in which dispersal occurs predominately in females (Smith 1974).

Howard (1960) suggested a genetic basis for dispersal in small mammals but it has proven very difficult to test his suggestion. Myers and Krebs (1971) provided the first genetic evidence that dispersing voles differed in allelic frequencies from voles which remained as residents in control areas. We have further substantiated this finding in our present work, but we have become skeptical of the utility of single-locus blood protein systems to get at Howard's suggestion. Our work with LAP is consistent with Howard's hypothesis, but we now require some technique for measuring dispersal directly for individual families so that we could estimate the heritability of dispersal tendencies. Techniques for *in utero* marking of the offspring of individual females would be necessary to do this in a field situation. Hilborn (1975) used an indirect tech-

nique to show that dispersal tendency was similar among siblings in four species of *Microtus* including *M. townsendii*.

Lidicker (1975) has reviewed the role of dispersal in small mammals, and concluded that many species of rodents may exhibit presaturation dispersal in which individuals emigrate before the population grows to maximum density. This type of dispersal can regulate population density below the limit set by food resources. Unfortunately, speculation about the consequences of different types of dispersal is tempered by a shortage of experimental work on field populations, and most of Lidicker's (1975) conclusions are only reasonable extrapolations from anecdotal natural-history observations. We need to study experimental designs that will enable us to measure dispersal directly and hence to test precise hypotheses about dispersal and population limitation.

The most impressive finding of this study is the similarity between our results on *Microtus townsendii* and the results of Myers and Krebs (1971) on *M. pennsylvanicus* and *M. ochrogaster*. This similarity suggests that the effects described here are real and need to be followed up by more detailed studies of the dispersal process and the behavioral concomitants of dispersal.

## Acknowledgments

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