Fates of disappearing individuals in fluctuating populations of *Microtus townsendii*

RAY HILBORN AND CHARLES J. KREBS
Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C., Canada V6T 1W5

Received May 26, 1976

HILBORN, R., and C. J. KREBS. 1976. Fates of disappearing individuals in fluctuating populations of *Microtus townsendii*. Can. J. Zool. **54**: 1507–1518.

Fates of disappearing individuals were determined for two natural populations of *Microtus townsendii* by livetrapping of evacuated areas and marginal habitat, and by marking individuals with radioactive tags to locate carcasses. Two hundred and nineteen out of the 454 individuals that disappeared were radioactively tagged during this 3-year study conducted in the University of British Columbia Research Forest near Haney, B.C. Only 30 radioactive tags were recovered on the live-trapping areas. Most disappearances in this vole population must have been caused by dispersal or predation.

Most disappearance from increase and peak populations was due to dispersal. Two summer periods of declining numbers were observed; during one such period many individuals' remains were found on the study areas, but during the other period of declining numbers few remains were found. There was no increase in dispersal rate as measured by the above techniques during either decline period. It is concluded that during the first brief period of declining numbers individuals were dying in their nests from physical factors associated with a severe summer drought and during the second period of declining numbers individuals were either moving long distances without going into traps or being taken by predators.

HILBORN, R., et C. J. KREBS. 1976. Fates of disappearing individuals in fluctuating populations of *Microtus townsendii*. Can. J. Zool. **54**: 1507–1518.

On a déterminé le sort d'individus disparus du sein de deux populations naturelles de *Microtus townsendii*, par capture d'animaux vivants dans des territoires évacués et les habitats marginaux, et par marquage radioactif permettant de localiser les carcasses. Durant cette étude de 3 ans, à la Station de Recherches Forestières de l'Université de Colombie-Britannique à Haney, 219 des 454 individus disparus avaient été préalablement marqués. Seulement 30 individus marqués ont été retrouvés dans les zones de capture. La plupart des disparitions, dans ces populations, sont probablement dues à la dispersion ou à la prédation.

La plupart des disparitions, dans les populations en recrutement ou les populations qui ont atteint leur sommet d'abondance, sont dues à la dispersion. On a par ailleurs remarqué que les populations avaient décliné durant deux étés; durant l'un de ces étés, on a retrouvé plusieurs carcasses d'individus dans les territoires étudiés, mais durant l'autre, peu de restes ont été retrouvés. On n'a pas enregistré d'augmentation du taux de dispersion par les techniques décrites ci-haut durant l'une ou l'autre de ces périodes. On conclut que durant la première période brève de déclin, les individus sont morts dans leur nid, à la suite de facteurs physiques associés à une sécheresse sévère et que durant la seconde période de déclin, les individus se sont déplacés sur de longues distances sans être capturés, ou alors ont été tués par des prédateurs.

[Traduit par le journal]

Introduction

To understand the factors determining the abundance of a species, one can either manipulate a population that is generally constant in numbers and observe the processes that return population density to its former level, or one can study a population fluctuating in numbers and observe the changes that occur between periods of increasing and decreasing numbers. Fluctuating species have been intensively studied; possibly because they are more noticeable during periods of abundance. Voles and lemmings (Rodentia; Cricetidae) are among the species that fluctuate dramatically in numbers. Vole outbreaks have been described throughout history (Elton 1942), and vole populations have long been of interest to ecologists.

Hypotheses to explain vole population fluctuations can be separated into two groups based on their prediction of the possibility of *in situ* mortality. *In situ* mortality is death of individuals on a study area as opposed to death by predation or dispersal. Predation and dispersal theories (Pearson 1966) predict that many individuals will disappear from an area entirely, and there will be little *in situ* death. Individuals eaten by weasels may die on the grids; however, their remains are distinguishable as weasel kills. In contrast, individuals that die from stress (Christian 1950), lack of food (Pitelka 1964), aggressive interactions, or because of genetic changes in viability (Chitty 1960, 1967) generally would die *in situ*. Christian and Davis (1964) suggest that "increased strife, with increased movement, will also increase losses through predation..." Declines caused by stress, lack of food, or genetic changes in viability do not require all losses to be *in situ* deaths, but *in situ* deaths should occur regularly in these declines. Stress, lack of adequate food, and genetic changes in viability may not be the proximate cause of death but should predispose the individual to natural agents of mortality, of which weather and disease might lead to *in situ* death.

In our study of dispersal and *in situ* death in *Microtus townsendii* populations we used three methods to determine the fates of disappearing individuals. First, in an attempt to separate deaths from emigration, individual animals were marked to provide information on the movement between adjacent study areas.

A second method of measuring dispersal is to remove individuals from an area and measure subsequent immigration into that area. This method assumes that a change in the rate of dispersal into an empty habitat is a measure of the change in dispersal tendency in control populations. This technique was used to measure dispersal in voles by Myers and Krebs (1971), and experiments of this type have been continued by Krebs *et al.* (1976).

A third way of measuring dispersal is to mark individuals with a radioactive tag and follow their movements with a Geiger counter. This method has been widely used to follow a limited number of individuals (Godfrey 1954; and Barbour *et al.* 1969); however, the probability of following an individual while it is actually dispersing is very small. An alternative method is to tag a large number of individuals radioactively and use the tag to recover the carcasses. Animals that die *in situ* should be recovered on the study area, whereas individuals that disperse or are taken by predators should not be recovered.

Methods

This study was carried out in the University of British Columbia Research Forest, located near Haney, B.C., 30 mi (48 km) east of Vancouver. The five study areas (A, B, P, Q, and Z) monitored during this 3-year study are shown in Fig. 1. Each grid was covered by a checkerboard of trap sites placed 7.6 m (25 ft) apart. Grids A and B were irregularly shaped, and each contained about 90 trap sites. They were located in two abandoned fields on an old homestead, were surrounded by 20- to 40-year-old coast forest and were monitored from May 1971 to June 1974. The low numbers of *Microtus townsendii* on these grids and the generally poor appearance of the grass suggested that these grids were poor *Microtus townsendii* habitat. We monitored these populations to determine if voles moved into marginal habitat as density increased. These populations were trapped every other week, except during the winter of 1971–1972 when deep snow prevented trapping for 6 weeks and during the last 6 months of the study, when they were occasionally trapped every 3rd week.

Grids P, Q, and Z were located 200 m from grids A and B, in a 50-acre area that had been logged and cleared in 1968 and subsequently seeded with natural grasses. Grid P was a 12 × 9 grid of traps, and grid Q was 10 × 10. Grids P and Q were the locations of the radioactive tagging experiments that were run from June 1972 to May 1974. The populations were trapped in the usual fashion except for the radioactive tagging.

Grid Z was trapped from July 1973 to June 1974; it

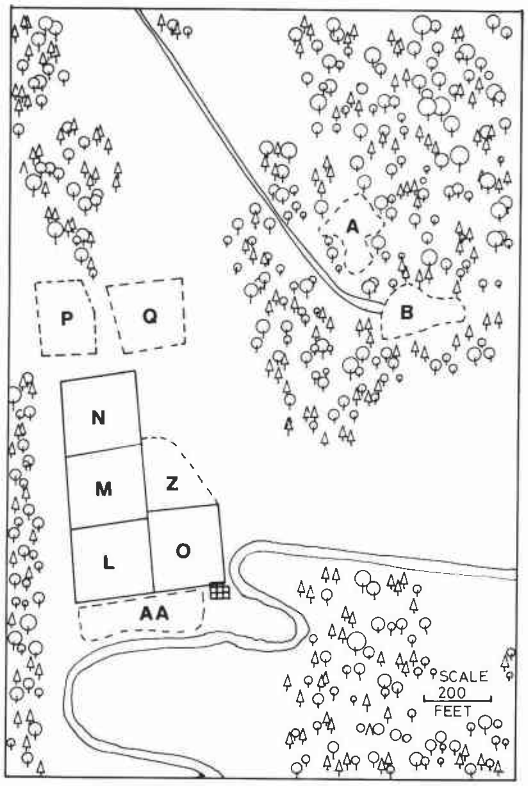

FIG. 1. Map of the study areas near Haney, B.C. Solid lines bounding study grids indicate mouseproof fence. Dashed lines indicate grid boundaries. Forested areas marked, blank areas indicate grassland.

was triangularly shaped, about 40 m from grid Q, and bounded on two sides by mouseproof fences used in other experiments. All individuals captured were processed as described below and removed following the method of Myers and Krebs (1971). Grid Z was continuously evacuated for measurement of immigration and dispersal.

Method of Trapping

The trapping method was identical to that used by Krebs *et al.* (1969). Each area was livetrapped with Longworth traps at each station on a biweekly schedule. These live traps were left permanently on the trapping areas, locked open when not in use, and covered with a heavy board. Traps were placed anywhere in the general vicinity of the trap station where sign of vole activity could be found. Whole oats and cotton were placed in each trap. Trapping was done for 2 days every 2nd week except on grids A and B as noted above. The traps were set in the afternoon, checked the next morning and again in the afternoon, and locked open during the third check on the next morning. During the summer, traps were set overnight only to prevent mortality from the heat. Using these techniques, we avoided almost all trap mortality and have been able to follow these populations year round.

Upon first capture each vole was tagged with a lettered and numbered fingerling-fish tag in the right ear and the following data were recorded at each capture: species; location on grid; weight; sex; scrotal or abdominal position of the testes in males; and vaginal orifice perforate or imperforate, nipples small, medium, or large, and pubic symphysis closed, slightly open or open in females. Weight was established to the nearest gram with specially constructed spring scales.

Few voles lost their ear tags, and those who did could usually be recognized from their sex, weight, and location on the grid. They were retagged and the appropriate change in number was recorded. Data recorded in the field were punched directly onto computer cards and then converted by a computer program to a standard numerical format for subsequent analysis.

Weather

The weather in the vicinity of Haney, B.C., is wet throughout the year with the exception of a usual 4- to 6-week dry spell during July and August. Precipitation averages well over 100 in. (254 cm) per year. Plant growth begins in March and is usually over by July, although some growth may take place during the fall. Because the water table is at the surface throughout most of the year and there is running water on the grids for at least 10 months of the year, the voles make their nests in grass clumps on the surface or in spaces between fallen logs and stumps. It rarely snows in the winter; however, during 1971–1972 trapping had to be suspended on grids A and B because of deep snow. On grids P, Q, and Z snow never interfered with trapping.

Radioactive Tagging

We used a radioactive tagging method to determine in which areas animals disappeared. We assumed that animals dying *in situ* would be recovered as carcasses or skeletons through their radioactive tags, whereas individuals that dispersed or were taken by predators would not be recovered. Table 1 summarizes the expected fates of radioactively tagged animals disappearing for different reasons.

Several different radioactive isotopes have been used for marking small mammals: cobalt, gold, iridium, and tantalum being the most frequent. Cobalt is no longer considered suitable because of its long half-life; gold is expensive; so iridium and tantalum have become the preferred isotopes for studies of this kind. Both have a half-life of about 6 months, are readily available in wire form, and are only moderately expensive. We used ^{182}tantalum, which was purchased in 50-cm spools with an activity of 200 μCi/cm. The wire consists of 0.2-mm central core of tantalum coated with a 0.1-mm layer of platinum, producing a wire 0.4 mm in diameter. We cut the wire into 0.75-cm lengths, and then wrapped these around the fingerling ear tags used to mark the voles. The wire was placed on the tag covering the 1000 digit, and then the entire wire and its area of contact with the tag were coated with epoxy glue. This method proved to be quite satisfactory. Each tag took about 1 min to make and cost about $2.00.

Grids P and Q were monitored as described in the section on trapping techniques. In addition to the normal tag placed on the right ear of the mouse, a radioactive tag was placed on the left ear. At every capture the mouse was checked to make sure the tags were still intact and any losses were noted. Losses of radioactive tags were quite rare and individuals were not retagged.

Method of Recovery

We walked slowly through each 25-ft^2 study grid, making sure that we were traveling within 1 m of each location on the grid. The tags could be detected at about 7 m and on two occasions we had co-workers hide 10 tags on the grids and were able to find each one without any trouble. All tags found were near the surface, and since tags were detectable through 2 ft of solid rock, we are confident that we have recovered all tags on the grids. An additional check on the method of detection is the recovery of tags known to have fallen off. During the study at Haney, eight tags were known to have been lost and all were recovered. We also searched a 10-m band around the perimeter of the study grids for any tags from individuals with home ranges on the edge of the grids.

Tests of the Radioactive Tagging Technique

We tested a number of assumptions about this technique. One assumption was that placing a radioactive tag on a vole did not affect its survival. Between July 1972 and July 1973, every third individual was not radioactively tagged to create a control population. Because of delays in the delivery of the isotope, various individuals were untagged throughout the study. The average probability of a radioactively tagged individual surviving for 2 weeks was 0.77 (219 individuals), while the probability of a non-radioactively tagged individual surviving was 0.78 (250 individuals). This suggests that radioactive tagging has little or no effect on survival.

As mentioned above, the radioactive tags occasionally fell off. So do non-radioactive tags, yet the loss rate seemed to be a bit higher for the radioactive ones, probably because of minor tissue damage in the vicinity of the isotope and greater weight of the radioactive tags. To estimate the biweekly rate of loss of radioactive tags, we divided the number of tags known to have been lost by the product of the number of sampling periods and the average number of radioactively tagged animals alive during each period. This is 8/549 or .015. Thus, we ex-

Table 1. Fates of radioactive tags for postulated ultimate causes of disappearance

Hypothesized cause of disappearance	Fate of carcass	Nature of tag recovery
Predation	Disappears	No sign except weasel kills, which are identifiable as such
Dispersal	Disappears	No sign
Starvation	*In situ* death	Found with skeleton
Stress	*In situ* death	Found with skeleton
Agonistic encounters	*In situ* death	Found with skeleton
Lowered viability due to genetic changes	*In situ* death	Found with skeleton

pected that 1.5% of individuals that disappeared would have lost their tags in the 2 weeks before their disappearance. Since we sampled biweekly and assumed that disappearance was random with respect to time of trapping, about 0.75% of animals that disappeared had lost their tags since the previous trapping period. Since not all individuals are caught each trapping period, this is an underestimate of the percentage of tags lost before disappearance and after last capture.

We assumed that when an animal died *in situ*, its carcass rotted and the tag and skeleton would be recovered. To test this we left 15 tagged carcasses in the field at different times of the year throughout the study. During the winter the carcasses decayed quite slowly; fungal growths reduced them in about 6 weeks. During the summer, carrion beetles attacked the carcasses right away and after a few days had usually eaten all the flesh. Only one of these carcasses was not recovered; it was presumably taken by a scavenger. Loss to scavengers could cause underestimation of the frequency of *in situ* death. However, since it apparently occurred infrequently and since the rapid rate of decay in the summer should reduce the proportion of carcasses taken by scavengers, we ignored it as a factor in this study.

Results

Population Fluctuations on Grids P and Q

The demographic attributes of the voles on grids P and Q seemed to be the same, and since the two grids were treated identically throughout this study, we have combined the data for most analyses. When trapping was begun in June 1972, no *Microtus townsendii* were present. They gradually colonized the area during the late summer and fall of 1972, reproduced during the next winter and spring, and reached a high of 115 voles by July 1973. During the entire 1st year of the study, the population maintained a geometric rate of increase averaging 18% biweekly. There was no brief decline in the spring of 1973 as reported by Krebs *et al.* (1969) for *Microtus pennsylvanicus*, and as found in *Microtus townsendii* in other areas around Vancouver. Figure 2 presents the minimum number of animals known to have been alive on grids P and Q. From the high of 115 in July of 1973, the population declined rapidly for 6 weeks to a low of 30; it then recovered to a level of 73 in late November. Numbers remained approximately

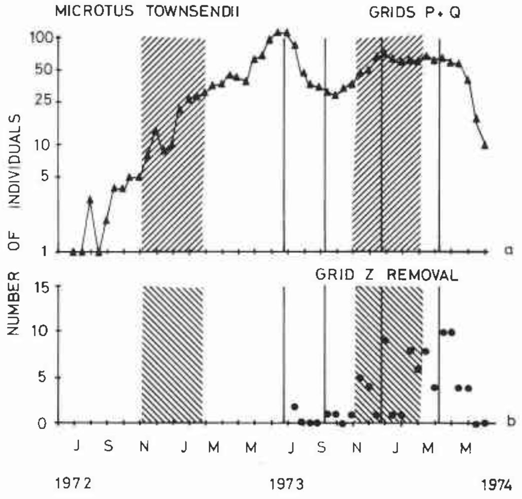

Fig. 2. (*a*) Minimum number of animals known to be alive on grids P and Q. (*b*) Number of animals trapped and removed on grid Z. Winter months of November–February are shaded. Vertical lines separate periods as defined within text.

TABLE 2. Population parameters for *Microtus townsendii* on grids P and Q

Period	Mean No. of adults	Mean rate of increase per 2 weeks	Index of juvenile survival	Adult immigration rate per adult	Minimum adult survival rate
I	18.1	0.18	2.7	0.13	0.84
II	47.9	−0.22	0.9	0.14	0.58
III	19.3	0.14	6.2	0.06	0.87
IV	30.0	−0.01	3.9	0.05	0.88
V	31.2	−0.29	2.3	0.10	0.60

constant from then until mid-April 1974 when they declined sharply and reached a low of 10 individuals at the beginning of June when the study ended.

We will consider two questions about the population fluctuations on the two control grids. (1) Why did the voles disappear during the two periods of declining numbers? (2) What were the fates of disappearing voles during the other periods?

We have chosen to combine the data into five periods, which we believe are characterized by their within-period similarities and between-period differences in survival. (To examine changes in reproduction, we would have used different period definitions to match the breeding seasons.) The periods are as follows:

Period	Interval	Population:
I	Jun. 1972 to Jul. 1973	increases
II	Jul. and Aug. 1973	declines
III	Sep. to Nov. 1973	increases
IV	Dec. 1973 to Mar. 1974	peaks
V	Apr. and May 1974	declines

Having selected the periods for pooling data, we calculated the relevant population parameters for each period. The calculation of survival rates in small mammals involves a number of assumptions, particularly if one wishes to separate losses caused by death from losses caused by dispersal.

Survival Rates

Table 2 summarizes the population parameters on grids P and Q by period. The survival index is the minimum adult survival rate. Minimum adult survival was high (0.84 to 0.88) in increase and peak periods I, III, and IV, and low (0.58 to 0.60) in decline periods II and V. During the 1st year of the study, survival was high and the population increased rapidly (up to the end of June 1973). Then the animals started to disappear at a very rapid rate. This was a general phenomenon in the vicinity of our study areas. A co-worker trapping enclosed populations of *Microtus townsendii* also reported very poor survival (0.72) during this period (Anderson 1975). Survival remained low for 8 weeks, then rose to its former high level and remained there throughout the fall and winter of 1973–1974. In April 1974 the survival rate dropped again and remained low until the end of the study. This second period of low survival was not as general as the first. Survival remained high throughout the spring inside the fenced areas (0.90), and on nearby unfenced area AA, (0.83), where the population increased rapidly at the same time as the population on grids P and Q were declining (Anderson 1975).

Immigration onto Grids P and Q

We define immigration rate for any trapping period as the number of newly tagged voles weighing more than 40 g, divided by the number of previously tagged voles weighing more than 40 g at the time. For a detailed justification see Hilborn (1974). The adult immigration rate is given in Table 2. Immigration was low during the first winter of the study. Up to the end of March 1973, we counted only 16 immigrants. During April, May, and June 45 animals immigrated. During the first two trapping periods of period II, immigration was still high (28 individuals), but it then dropped off for the rest of the study. During periods III, IV, and V there were less than four immigrants per week.

Intensity of Breeding

Table 3 summarizes several indices of breeding intensity by period. We use four indices of reproductive intensity: percentage of adult females with medium or large nipples; number of fe-

TABLE 3. Indices of reproductive intensity for adult (> 43 g) females. Individuals are considered separately at each capture. Percentages are given in parentheses

Period	*N*	No. of females lactating	No. of females pregnant	No. of females with open symphysis	No. of litters in traps
I	204	55 (27)	36 (18)	10 (5)	3 (1)
II	103	24 (23)	9 (9)	9 (9)	0 (0)
III	43	6 (14)	7 (16)	3 (7)	2 (5)
IV	56	7 (13)	9 (16)	6 (11)	4 (7)
V	68	14 (20)	20 (29)	4 (6)	1 (1)

males obviously pregnant; number of females with pubic symphysis open; and number of females giving birth in traps. These indices show that females were breeding during each period. Most breeding during the study occurred in the spring and fall. Figure 3 shows the percentage of adult females with medium or large nipples, which is the most reliable index of reproduction. There was active breeding in the two periods of declining numbers (summer 1973 and summer 1974), so lack of breeding cannot account for the dramatic declines in numbers.

Recruitment

Table 2 shows the index of juvenile survival. The index of juvenile survival is defined as the number of newly tagged juvenile and subadult voles divided by the number of females lactating 4 weeks previously. This index has been used in the past by Krebs (1966 and later papers) to estimate survival of young voles from birth to first capture.

Tables 2 and 3 indicate that this population increased in 1972 and 1973 under the joint influence of normal reproduction and good juvenile and adult survival. The decline in summer 1973 was precipitated by a drop in both juvenile and adult survival, while reproduction continued at normal rates. Juvenile and adult survival improved in the fall of 1973 but reproduction fell off during the winter of 1973–1974. The population declined dramatically in summer 1974 under the pressure of poor survival in adults and juveniles but normal reproductive rates.

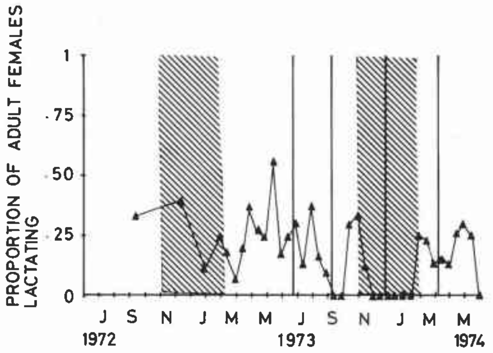

FIG. 3. Proportion of adult females (> 43 g) lactating on grids P and Q. Winter months of November–February are shaded.

Radioactive Tagging Results

During this study, 219 voles were radioactively tagged and later disappeared. Only 15 of these voles were recovered as carcasses or skeletons, indicating definite *in situ* mortality, 11 tags were recovered that showed no sign of the fate of their former bearer, and four tags were recovered in weasel nests (Table 4).

From the number of radioactively tagged voles that disappeared and the number of recoveries in each classification given in Table 4, we divided deaths into three types; carcasses or skeletons (*in situ* death), no sign at site of recovery (unknown fate), and recoveries in weasel nests. Percentages for each are given in Table 4.

From the 219 radioactively tagged voles that disappeared 30 of the tags were recovered. Almost all *in situ* death occurred during the sharp decline in the summer of 1973 (period II). *In situ* death appears to have been an unimportant mortality factor during any other period. The two decline periods (II and V) show striking differences in *in situ* mortality rates, which suggests very different mortality agents during those two periods. Individuals that died *in situ* were found as complete skeletons with both the radioactive and normal ear tag neatly bundled inside a vole nest. In a few nests, in addition, a non-

TABLE 4. Recoveries of radioactively tagged individuals

Period	No. of radioactively tagged individuals disappearing	Carcasses or skeletons found	No sign (unknown fate)	Weasel kills
I	40	1	2	0
II	37	10	4	0
III	11	0	1	0
IV	40	2	3	0
V	91	2	1	4
Total	219	15	11	4

radioactively tagged vole was also found dead in the nest. This type of nest mortality was rare during period V.

To determine what happened to the large number of tags not recovered on the grids, we searched surrounding areas at the end of the study. We classified the areas that were not part of grids P and Q into three types: grassland, forest, and plantation. The grassland occurred near grids P and Q as seen in Fig. 1. There were about 20 acres of plantation nearby and an endless supply of forest. We searched 20% of the surrounding grassland, 5% of the surrounding plantation, and about 5% (1 acre) of the nearby forest. It is difficult to determine what constitutes 'nearby' for the forest so that this estimate of 5% should be used with caution. Assuming that all the tags not recovered from period V ended up in only one of these habitats, the number of tags we should have recovered in that habitat is listed below.

Habitat	% searched	No. tags expected
Grassland	20	16.8
Forest	5	4.2
Plantation	5	4.2

Thus it appears that we would have found some tags if there had indeed been any in these areas, provided the tags were not concentrated in one place (e.g., in a few predator nests). In fact, we recovered no tags during these searches, which suggests that most animals either dispersed very long distances (more than $\frac{1}{2}$ mi) or were taken by avian predators. Even if some of these tags had been recovered, it might have been difficult to determine the agent of mortality. In any case, our estimates of *in situ* mortality rates would not have been affected.

Removal Experiments—Grid Z

Trapping was begun on grid Z in June 1973, after 2 weeks of prebaiting. In the first two trapping periods 56 voles were removed, a density equivalent to that on grids P and Q at the same time. Figure 2 shows the number of voles removed from grid Z in each trapping period. This initial clearing off is not shown in Fig. 2. The data are summarized in Table 5. The number of animals that disappeared from grids P and Q and the number of disappearing voles that were captured on grid Z are also presented. During the two periods of decline very few disappearing individuals showed up as removals (0 to 0.05), but during the increase and peak periods the percentage was much higher (0.18 to 0.24). An index of dispersal (the number of removals divided by the number of disappearing voles from grids P and Q) is given and shows the same trend: low during the declines, higher during the peak period IV, and highest during the increase period III. The removal experiment on grid Z demonstrates that dispersal to evacuated areas can account for a sizeable proportion of loss from increasing and peak populations but for a small portion of the loss from declining populations. These results are in complete agreement with similar experiments by Myers and Krebs (1971) and more recently published work by Krebs *et al.* (1976).

Movements Between Grids

In this study, 25 individuals moved between grids P and Q. Assuming that an individual was no more likely to move from grid P to grid Q than it was to move from grid P to another area in some other direction, we have used the rates of movement between grids as an index of dispersal to similar habitat nearby. Table 6 presents the number of known movements by period. Also shown are two rates of movement: (1) the probability that an individual alive on one of the two areas would move to the other area during any trapping period, and (2) the proportion of disappearance that could be accounted for by known movements between grids.

The proportion of disappearance owing to movement between grids was high during increase periods (0.10 to 0.12), and low during the peak and decline periods (0.02 to 0.04). This presents the same pattern for dispersal as shown in Table 5. Since grid Q represents only a small portion of the available grassland for individuals

TABLE 5. Results of removal experiments on grid Z

Period	No. disappearing from P and Q	No. of tagged removals	Proportion of disappearance from grids P and Q found on grid Z	Total No. of removals from grid Z
I	134			
II	126	0	0.00	2
III	33	8	0.24	24
IV	55	10	0.18	26
V	106	5	0.05	28

TABLE 6. Movements between grids P and Q

Period	No. moved between grids	Probability of movement from one grid to the other in any trapping period	Proportion of loss accounted for by movement
I	13	0.018	0.10
II	2	0.006	0.02
III	4	0.013	0.12
IV	2	0.004	0.04
V	4	0.016	0.04

emigrating from grid P and vice versa, the actual number of emigrants from these grids should be the number of known movements multiplied by some constant. Because the probability of dispersal between two points is likely to be a function of the distance between these two points and the shape of this function is unknown, we have not attempted to estimate this constant.

Grids A and B

Grids A and B (see Fig. 1) were trapped from May 1971 to June 1974. The cover on these two grids was quite different from that on all other grids at Haney and throughout the Vancouver area. The grass on these two grids grew very low to the ground, had a large amount of moss mixed with it, and lacked enough litter to provide cover for potential runways. Most of the *Microtus townsendii* captured on these two grids lived in one section of grid B, which had an exceptionally thick moss cover in which the voles constructed runway networks.

When trapping was initiated there were 10 to 15 *Microtus townsendii* on these two grids. Numbers remained in that range throughout the summer and into the fall of 1971, but declined during the winter and by spring had fallen to zero. During the last 2 years of the study, when grids P and Q were going through their fluctuations, five *Microtus townsendii* were trapped on grids A and B. All of these voles appeared between May and August 1973, which coincides with the pulse of immigrants to grid Z. It seems unlikely that the 50 m of woods separating the fields of grids P and Q from grids A and B would act as a major barrier to immigration (one individual is known to have dispersed 1 km from grid P to another study area). We believe that the sample size in these data is insufficient for any firm conclusions about rates of dispersal into marginal habitats. At the same time, it is clear that there was no large-scale dispersal into this marginal habitat during the two population declines observed on grids P and Q.

Nature of the Declines

Chitty (1955) has defined three types of microtine declines based on the rate of population decrease and the timing of the decline. Type H declines involve a gradual decline in numbers over 1 or more years with a possible slight recovery during the intervening breeding season. Type G declines are more abrupt, occur over no more than 1 year, and are not followed by recovery during the breeding season. Type M declines are very rapid population decreases associated with winter and early spring. Krebs and Myers (1974) have classified 36 recorded declines from the literature into 18 type H, 13 type G, and 5 type M declines. Most declines are preceded by a peak period of high numbers, but there are several recorded instances of declines beginning during an increasing population without a peak period (Krebs 1966, Tilden control grid). A period of low numbers following a decline is another variable feature of microtine fluctuations. Populations may reach low numbers at the end of a decline and remain there for 1 or 2 years, or may recover immediately from a decline (Chitty 1952; Krebs *et al.* 1969; Krebs and Myers 1974). The rapid recovery from period II is consistent with this phenomenon. During a peak period, a short period of declining numbers may occur in the spring at the onset of reproduction. This 'spring decline' has been well documented by Krebs *et al.* (1969) and occurred in other *Microtus townsendii* populations in the Vancouver area (LeDuc and Krebs 1975). The spring decline may involve very poor survival and rapid decrease in numbers for 1 or 2 months, but usually recruitment and immigration rapidly compensate for the losses.

What is the relationship between the two declines we observed in this study and the general attributes of declines in voles and lemmings? Neither decline fits into the categories described by Chitty (1955). The rates of decline are as high as recorded for any of the type M declines, yet neither decline occurred during the winter or early spring. The first decline in period II occurred during midsummer. The second decline in period V occurred during late spring and early summer. It did not resemble a spring decline, since breeding began 2 months before the population started to go down. Then the population declined to such a low level that rapid recovery, normal for a spring decline, would have been possible only by extensive immigration. The high survival rates on nearby unfenced grid AA during period V (0.83) and fenced grid O (0.90) also suggest that this decline on grids P and Q was not the typical spring decline observed in the Vancouver area, where survival is reduced on adjacent areas (LeDuc and Krebs 1975). The first decline, period II, is similar to the usual spring decline in that it was very brief and recovery from low numbers was quite rapid, except that it occurred in the middle of the summer breeding season. The second decline was most similar to the declines observed in Indiana by Krebs *et al.* (1969). It was preceded by a period of peak numbers and reached very low numbers. The major difference between the period V decline and those observed in Indiana was the high rate of decrease. None of the spring–summer declines observed by Krebs had quite as high a rate of loss.

Causes of Disappearance

The rates and estimated causes of disappearance are summarized by period in Table 7. The total rate of loss is 1.0 minus the minimum survival rate. The loss rate owing to dispersal is the immigration rate from Table 2. The *in situ* death rate (from Table 5) is the proportion of disappearing radioactively tagged voles recovered as skeletons or carcasses times the total rate of disappearance. The unknown column is the total rate-of-loss column minus the sum of dispersal and *in situ* losses. We chose immigration rates instead of removals from grid Z or known movements between grids P and Q because the immigration estimates involved greater sample sizes and are a more direct estimate of dispersal. Although the calculation of immigration rates into grids P and Q involved a number of assumptions (see Results section for details), the estimation of dispersal by this method agreed with the two other methods of estimating dispersal, so that we feel it is probably reasonable.

The *in situ* death rate presented in Table 7 is a minimum estimate. Loss of tags since final capture, removal of carcasses by scavengers, and failure to detect carcasses or skeletons would reduce the estimate of *in situ* death rate. However, the data presented earlier suggest that these three factors are probably unimportant. At most, the estimate of *in situ* death rate could be a 60% underestimate, since 40% of known tag losses were recovered as carcasses or skeletons during period II. Assuming that the estimate is 50% low, at worst, *in situ* death is still insignificant

TABLE 7. Rates of disappearance in *Microtus townsendii*. Total is 1.0 − minimum 2-week survival rate. Dispersal is immigration rate from Table 3. *In situ* death and unknown columns are from Table 5

Period	Total	Dispersal	*In situ* death	Unknown
I	0.16	0.13	0.005	0.025
II	0.42	0.14	0.113	0.167
III	0.13	0.06	0.000	0.070
IV	0.12	0.05	0.006	0.064
V	0.40	0.10	0.008	0.292

except during period II, during which *in situ* death accounted for almost all mortality. The actual rate of *in situ* death is probably somewhere between the values presented in Table 7 and twice those values.

The following generalizations can be made from Table 7. The decline during period II can be attributed to a very high rate of *in situ* death, but the causes of increased losses in period V are unknown. The unknown causes (outlined in Table 1) are either dispersal or predation. The indices of dispersal we have calculated indicate that dispersal rates did not go up during period V. We are left with two possibilities; either the losses during period V were due to increased predation rates, or the voles were dispersing and not entering traps.

We have no method of measuring loss caused by predation. Recoveries of radioactive tags from weasel nests were very infrequent. No systematic observations of avian predators were made during this study. In more than 3 years of field work at Haney, we sighted only three hawks or owls, which suggests that raptors take few voles from our study areas. Nocturnal raptors, however, could be important. Only two weasels were captured in mouse traps during this study: one during period II and one during period IV. At another location near Vancouver, 11 weasels were caught on a single morning, indicating that if large numbers of weasels were present on the grids, they would have been caught. In addition, it seems unlikely that the decline on grids P and Q in period V was due to increased predation when the population on unfenced grid AA (located less than 200 m away) maintained high survival throughout this period. Some other explanation is required.

It is possible that stress, shortage of food, or genetic changes increased vole mortality by causing more movement and greater vulnerability to predation, yet it seems unlikely that there would not be some *in situ* death during declines owing to these causes. It thus appears unlikely that any of the above agents caused the reduced survival in period V. Similarly, loss owing to predation appears to be untenable. The high rate of *in situ* death during period II suggests that stress, starvation, or genetic changes in viability predisposed the individuals to mortality agents during this period, but, again, there is reason to doubt this. All of these mechanisms imply a gradual change in the population or its food supply. Yet there was no peak period and the survival went from very good to very poor in a 2-week period. Poor survival occurred on six grids (fenced and unfenced) at Haney with widely differing density histories. The 6 weeks of poor survival in period II occurred during an unusually hot and dry part of the summer, and the data imply some sort of external mortality factor. It is possible that shortages of water or extreme temperatures were responsible for the reduced survival during period II. Voles were frequently parasitized by botflies during this period, which could be viewed as a contributing factor to the low survival; but other populations monitored at the same time near Vancouver were also infested with botflies and showed no similar decline in the summer of 1973. We have no explanation for the decline in period V. We have ruled out every mortality agent described in the introduction to this work and are left with the poor explanation that individuals dispersed during period V without entering traps on evacuated areas. Calvert (1976) described a decline in a fence-row population of *Microtus townsendii* that was very similar to the decline we observed in summer 1974.

Krebs *et al.* (1973) have considered the very brief declines similar to that in period II to be a seasonal phenomenon and unrelated to the causal relationships determining microtine fluctuations. They would not consider the different mortality factors between the two periods of decrease to be evidence that there is not a single underlying cause of microtine fluctuations. Myers and Krebs (1971) and Chitty and Phipps (1966) rejected dispersal as a causal agent for the disappearance during the declines and suggest that either *in situ* mortality or long-range nontrappable dispersal occurs. *In situ* mortality occurred in period II (demonstrated by direct measurements). At present, we are forced to accept long-range dispersal as the only remaining explanation for period V. We suggest that voles move from their home ranges and cross habitats empty of other animals, not stopping to investigate traps. They presumably move long distances and, while most are lost on the way, a few may survive to colonize distant locations. This suggestion is uncomfortably close to the mythical lemming march-to-the-sea story and requires confirmation by new experiments on dispersal.

The idea that small mammals may disperse long distances is not new. Murray (1967) suggested a mechanism that encourages long dis-

TABLE 8. Characteristics of the phases of *Microtus townsendii*

Phase	Rate of population increase per 2-week period	Possible duration, weeks	Time of year	Maximum body weight during period, g	Index of juvenile survival	Minimum survival rate per 2 weeks
Increase	0.14–0.18	14–52	Year round	70–80	2.7–6.2	0.84–0.87
Peak	0.0	14	Fall and winter	50–60	3.9	0.88
Decline	−0.29	10 or more	Spring and summer	40–50	2.3	0.60
Brief summer decline	−0.22	6–8	Midsummer	40–50	0.9	0.58

tance dispersal through aggression and territoriality. Lidicker (1962) considered the possibility that dispersal acted as a regulatory mechanism, and Howard (1960) proposed that group selection caused individuals to disperse. The unknown nature of trap response makes the results of our experiments difficult to interpret in light of the above proposals.

More data would be required to determine if the brief decline in the summer of 1973 was a seasonal phenomenon or part of the demographic changes associated with long-term fluctuations in *Microtus townsendii.* Several types of experiments might provide further information on the causes of disappearance of animals during declines similar to that of period V. One method would be to monitor enclosed populations with emigration permitted via exit doors and then shut the exits when a decline is anticipated. If animals were dispersing but not trapped, the population would either fail to decline, or the animals would die *in situ.* This method has been suggested by Myers and Krebs. A second method would be to use radio monitoring of large numbers of voles, but this is difficult with present technology. Myers and Krebs (1971) suggested setting drift fences to force dispersing individuals into areas of intensive trapping. Such an experiment would require a large number of fences and some sort of pitfall trap to capture individuals that would not explore normal live traps. Pitfall trapping was not possible in this study because of the high rainfall and soil moisture. Radioactive tagging of a population on a small island might also provide clues about the fates of disappearing individuals, although the "fence effect" discussed by Krebs *et al.* (1969) may well occur there too.

Populations of *Microtus townsendii* in the Vancouver region fluctuate in size from year to year but do not show all the attributes of a classically cyclic microtine population. Table 8 is a summary of the attributes of the population phases of *Microtus townsendii* from this study. We defined four phases: increase, peak, decline, and brief summer decline. We used periods I and III as increase periods, periods IV as a peak period, period V as a decline, and period II as a brief summer decline. This table represents the first step towards a description of the demographic attributes of the different phases of *Microtus townsendii.* Other work currently under way on *Microtus townsendii* will further contribute to this table, particularly by comparing the brief summer decline with the spring decline. We hope that differences between the various types of declines will help elucidate their causes and that our study will serve as a caution to future students of agents of mortality: do not assume that all declines have a common cause.

Acknowledgements

We thank the National Research Council of Canada for financial support during this research. The University of British Columbia Research Forest provided the field facilities. Judith Anderson, Alan Birdsall, Rudy Boonstra, Dennis Chitty, Pam Fraker, Janice LeDuc, Jim Redfield, Suzanne Robertson, Tom Sullivan, Conrad Wehrhahn, Irene Wingate, and Ralf Yorque provided field assistance or comments on this manuscript.

ANDERSON, J. 1975. Phenotypic correlations among relatives and variability in reproductive performance in populations of the vole *Microtus townsendii*. Ph.D. thesis, University of British Columbia, Vancouver.

BARBOUR, R. W., M. J. HARVEY, and J. W. HARDIN. 1969. Home range, movements, and activity of the eastern worm snake, *Carphophis amoenus amoenus*. Ecology, **50**: 470–476.

CALVERT, M. F. 1976. Population dynamics of *Microtus townsendii* in a linear habitat. M.S. thesis, University of British Columbia, Vancouver.

CHITTY, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–1939. Phil. Trans. R. Soc. B, **236**: 505–552.

——— 1955. Adverse effects of population density upon the viability of later generations. *In* The numbers of man and animals. *Edited by* J. B. Cragg and N. W. Pirie. pp. 57–67.

——— 1960. Population processes in the vole and their relevance to general theory. Can. J. Zool. **38**: 99–113.

——— 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Australia, **2**: 51–78.

CHITTY, D., and E. PHIPPS. 1966. Seasonal changes in survival in mixed populations of two species of vole. J. Anim. Ecol. **35**: 313–331.

CHRISTIAN, J. J. 1950. The adreno-pituitary system and population cycles in mammals. J. Mammal. **31**: 247–269.

CHRISTIAN, J. J., and D. E. DAVIS. 1964. Endocrines, behavior, and population. Science, **146**: 1550–1560.

ELTON, C. 1942. Voles, mice and lemmings. Clarendon Press, Oxford.

GODFREY, G. K. 1954. Tracing field voles (*Microtus agrestis*) with a Geiger-Muller counter. Ecology, **35**: 5–10.

HILBORN, R. 1974. Fates of disappearing individuals in fluctuating populations of *Microtus townsendii*. Ph.D. thesis, University of British Columbia, Vancouver.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. **63**: 152–161.

KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. **36**: 239–273.

KREBS, C. J., M. S. GAINES, B. L. KELLER, J. H. MYERS, and R. H. TAMARIN. 1973. Population cycles in small rodents. Science, **179**: 35–41.

KREBS, C. J., B. L. KELLER, and R. H. TAMARIN. 1969. *Microtus population biology*: demographic changes in fluctuating populations of *Microtus ochrogaster* and *Microtus pennsylvanicus* in Southern Indiana. Ecology, **50**: 587–607.

KREBS, C. J., and J. H. MYERS. 1974. Population cycles in small mammals. Adv. Ecol. Res. **8**: 267–399.

KREBS, C. J., I. WINGATE, J. LEDUC, J. A. REDFIELD, M. TAITT, and R. HILBORN. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. Can. J. Zool. **54**: 79–95.

LEDUC, J. and KREBS, C. J. 1975. Demographic consequences of artificial selection at the LAP locus in voles (*Microtus townsendii*). Can. J. Zool. **53**: 1825–1840.

LIDICKER, W. Z. JR. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Am. Nat. **96**: 29–33.

MURRAY, G. G. JR. 1967. Dispersal in vertebrates. Ecology, **48**: 975–978.

MYERS, J. H., and C. J. KREBS. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. **41**: 53–78.

PEARSON, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. J. Anim. Ecol. **35**: 217–233.

PITELKA, F. A. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. I. Introduction. *In* Grazing in terrestrial and marine environments. Blackwell Publications, Oxford. pp. 55–56.