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## DEMOGRAPHY OF THE SPRING DECLINE IN POPULATIONS OF THE VOLE, *MICROTUS TOWNSENDII*

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### SUMMARY

(1) Population densities of small rodents typically decline in the spring at the start of the breeding season. Eighteen spring declines of *Microtus townsendii* were monitored by mark–recapture methods on undisturbed grasslands near Vancouver, British Columbia.

(2) The duration and size of spring declines is highly variable: sometimes there is virtually no decline, and at other times more than 90% of the population may be lost in a spring decline that may last for 12 weeks after breeding begins.

(3) Males usually disappear more rapidly than females.

(4) The size of the spring decline is closely related to the rate of loss.

(5) In light-to-moderate spring declines most of this loss is due to emigration; in severe declines most loss is due to death rather than movement.

(6) In males, the amount of rump wounding is highly correlated with the size of the spring decline.

(7) We suggest that spring declines in both sexes of *M. townsendii* are produced by spacing behaviour, but we do not know if differences in spacing behaviour are sufficient to explain all variations in spring declines.

### INTRODUCTION

Populations of many species of voles, mice, and lemmings may decline substantially in late winter and early spring (Sadleir 1965; Chitty & Phipps 1966; Watts 1969; Fairbairn 1977). These declines span the late winter, when the animals are not breeding, and the early spring, when they have just started to breed. These spring declines are believed to be a result of socially-induced mortality or dispersal caused by spacing behaviour among animals coming into breeding condition (Krebs, Halpin & Smith 1977). Direct evidence for this proposed explanation for spring declines is not available for voles. In this paper we provide a detailed demographic analysis of spring declines for three populations of *Microtus townsendii* (Bachman) near Vancouver, British Columbia.

### METHODS

The study areas and the trapping techniques have been described in LeDuc & Krebs (1975) and in Krebs *et al.* (1976). Three grassland areas were trapped: Westham Island,

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Ladner Air-base, and Serpentine Fen. Only data from unmanipulated populations were used for this analysis. Trapping areas each covered 0.8 h of grassland with 100 trapping points spaced 7.6 m apart. One or two Longworth live-traps were left permanently at each trapping point, and were locked open when not in use. When first caught, voles were marked with a fingerling fish tag in the right ear; we noted weight, sex, and breeding condition, and then released the vole immediately. Traps were set for 2 days every second week. Population parameters were obtained by enumeration, which is probably an accurate method in the spring, when few juveniles are present.

## RESULTS

Figure 1 illustrates the type of demographic data analyzed below. The spring decline in 1973 on grid I was particularly striking, since it continued for 20 weeks. From peak numbers of 93 males and 138 females on this 0.8-h grid in mid-December 1972, numbers fell to 14 males and 33 females in early May 1973. This spring decline can be subdivided into two parts (Fig. 1). The first half, until mid-February, occurred with virtually no voles

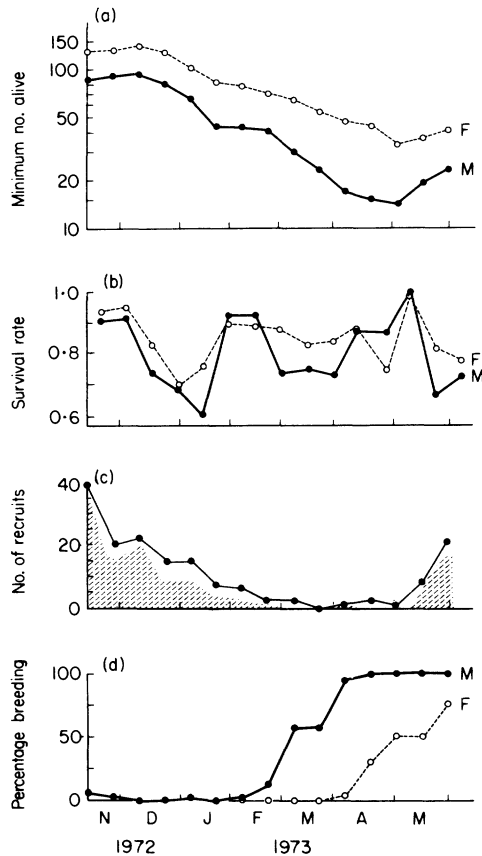


FIG. 1. A severe spring decline in *Microtus townsendii* in 1973 on Westham Island, Grid I. Density (a) is expressed per 0.8 h trapping area, survival (b) as finite rate per 2 weeks. Recruitment (c) is the number of untagged voles caught (shaded area represents young voles < 40 g). Reproduction (d) is measured by descended testes in males and lactation in females. Male numbers fell at 10% per week and female numbers at 7% per week for 20 weeks. M, male; F, female.

breeding. The second half of the decline, after mid-February, spanned the start of the breeding season. The rate of population decline tends to increase once breeding begins. In this example numbers were falling at 7–8% per week before breeding began and at 8–11% per week after breeding started. The rate of decline of the two sexes need not be equal. In Fig. 1 males declined 2–3% per week faster than females. Survival rates also varied between the sexes; for 6 weeks from the start of breeding in March males survived 10% less well than females for 6 weeks. Few new juvenile voles come into the trappable population during a spring decline, although unmarked adult voles from the previous breeding season may be recruited (probably through immigration) during the decline.

Eighteen spring declines of the type shown in Fig. 1 have been studied from 1971 to 1976. Table 1 summarizes the population parameters that we have measured during spring declines. The duration of spring declines is highly variable. Males typically decline in numbers more rapidly than females. Recruitment of small-sized voles is very low at this time of year but some recruitment by immigration of adults does occur. Females outnumber males at the start of the decline, and even more so at the end of the decline.

TABLE 1. Range of demographic parameters found in eighteen examples of spring declines, *Microtus townsendii*. Parameters obtained by enumeration on trapping areas of 0.8 hectare; a recruit is any untagged vole

	Mean	Range
Duration of decline (weeks)		
total	16.2	8–22
breeding season	11.7	8–20
Density at start of decline		
males	80.9	9–159
females	87.4	18–192
Rate of change per week*		
males	–0.074	–0.264 to +0.024
females	–0.045	–0.124 to +0.013
Probability of survival per 2 weeks*		
males	0.73	0.37 to 0.90
females	0.84	0.59 to 0.90
Number of recruits < 40 g per 2 weeks*	2.8	0.4–7.2
Total number of recruits per 2 weeks*	7.4	1.0–22.1
Average body weight of males at start of decline*	51.2	35.7–66.5
Sex ratio (% males) at start of decline*	44.1	31.4–57.8

\* For breeding season part of spring decline only.

We have explored the associations among the variables summarized in Table 1 by a simple correlation analysis in order to describe in more detail the anatomy of spring declines. The percentage fall in numbers during a spring decline is closely related to the rate of decline per week ( $r=0.88$ ,  $n=18$ ) but not to the duration of the decline ( $r=0.22$ ). We will thus use the instantaneous rate of decline per week as a measure of the size or intensity of spring declines. The rate of decline in the non-breeding period was correlated with the subsequent rate of decline in the breeding period ( $r=0.72$ ,  $n=11$ ), and a slightly better correlation occurred between the rate of population decline in males and the rate of decline in females ( $r=0.79$ ,  $n=18$ ) during the breeding period. In two cases males declined in numbers in the spring but females did not, and in one case females declined but males did not.

The intensity of the spring decline in *Microtus townsendii* is more closely related to the

loss rate than to the recruitment rate. For males, the correlation between intensity of decline and probability of survival is 0.89, for females 0.79. The loss rate is made up of both death and emigration. We can separate these two factors if we assume that recruits during the breeding portion of the spring decline are all immigrants, and that they equal the number of emigrants from the study area. Emigration estimated in this way refers only to successful emigration of trappable animals and voles killed while moving from one area to another or failing to enter traps are included as deaths. We cannot test this critical assumption directly. If it is correct, we would expect the number of emigrants during the spring decline (calculated as described above) to be closely related to the number of immigrant voles colonizing an adjacent vacant area at the same time. We compared these two estimates for the two control grids which had removal areas adjacent to them (see Krebs *et al.* 1976 for details of the removal areas), and found a high correlation ( $r=0.93$ ,  $n=9$ ). These results support the assumption that emigration equals immigration at this time of the year.

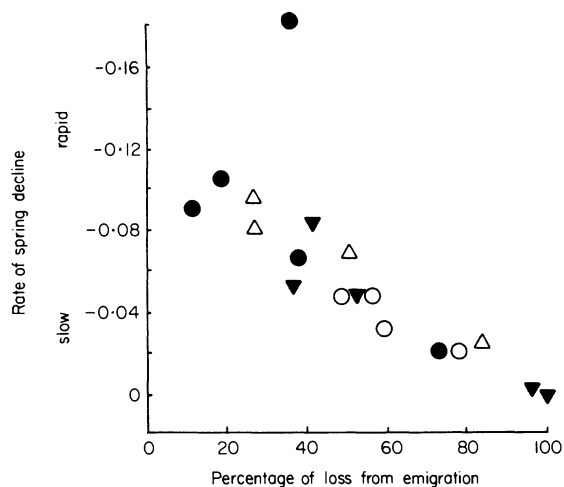


FIG. 2. Relationship between the percentage of losses due to successful emigration and the rate of the spring decline in *Microtus townsendii*. The rate of spring decline is the instantaneous rate of population change per week. ● Grid I, ○ Grid C, ▼ Grid E, △ other Westham Island grids.

The most severe spring declines all involved little emigration and hence (by inference) much mortality (Fig. 2). Many of the slight spring declines are only social reorganizations with many individuals leaving one area and settling successfully in another. Severe spring declines are clearly due to mortality and not simply to social reorganizations with little loss. This conclusion seems to hold for both males and females because the relationship in Fig. 2 fits the data both for males and for females.

Body weight distributions of *M. townsendii* vary greatly from spring to spring (Chitty & Chitty 1962), and we have searched for associations between the intensity of the spring decline and the weight distribution among males in February and March. We can find no significant correlation between any parameter of the weight distribution and the intensity of the spring decline in the same year. In particular, spring declines are neither bigger nor smaller than average in years when large *M. townsendii* are common (individuals > 70 g).

We then considered the hypothesis that the weight distribution of voles in one spring predetermines the size of the spring decline for the *following* year. Chitty (1952) was the

first to suggest this mechanism. All lag correlations between body weight parameters in year  $t$  and intensity of spring decline in year  $(t+1)$  were significant. For example, the larger the proportion of male voles above 70 g in March, the more intensive was the spring decline in the following year ( $r = -0.91$ ,  $n = 11$ ,  $P < 0.001$ ). Populations with large-sized males thus are programmed to drop sharply in numbers the *following* spring.

If spacing behaviours are an important component of spring declines, we might expect the bigger declines to be associated with more wounding. We counted all visible skin wounds by scanning the rump area of all voles live-trapped from May 1974 onward. Data from five complete spring declines spanning 2 years on three areas are available.

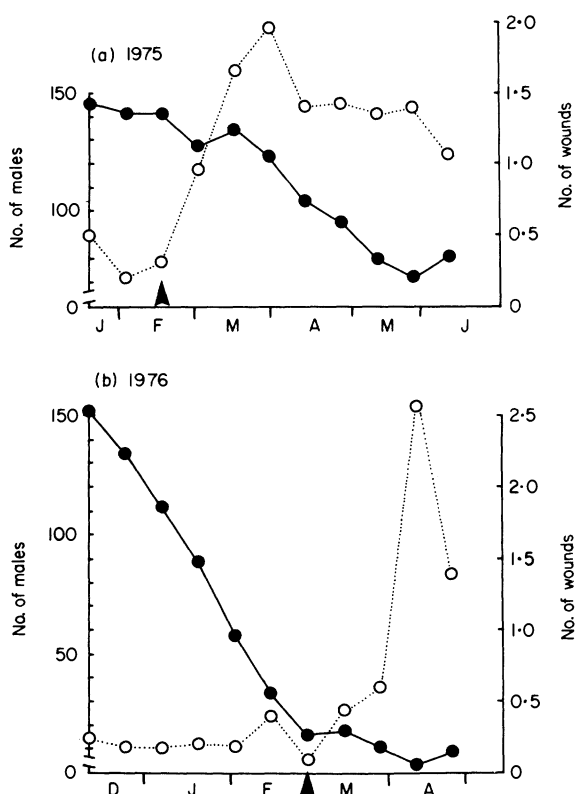


FIG. 3. Changes in male population density (●) and average number of wounds on the rump (○) during two spring declines on grid I. (a) shows the moderate-sized 1975 decline (4% per week) and (b) shows the severe 1976 decline (18% per week). Arrows indicate the start of the breeding season.

Figure 3 shows the pattern of changes in the amount of wounding during two spring declines of differing intensity. Wounding is always rare during the winter but always builds up rapidly after breeding starts in the spring. We use the maximal value of wounding observed during the spring decline as an index of the intensity of agonistic interactions. In males the number of wounds is highly correlated with the rate of the spring decline after breeding begins ( $r = -0.93$ ,  $n = 5$ , holding the density at the start of the decline constant). Thus for males, the more the wounding, the more rapid and prolonged is the spring decline. The same association is not evident for females, which rarely show wounds on the rump.

Finally, we looked for individual correlates of survival during the spring decline by comparing the following characteristics of voles which *did* and voles which *did not* live through a spring decline: body weight at start of decline, week of first capture (index of age), number of wounds received during the decline, and breeding condition during the decline. The last two variables were determined by averaging the data for each individual over all his captures during the decline. During slight spring declines (e.g. Fig. 3 top) larger males and females survived significantly better than smaller voles, and these survivors were more often captured in breeding condition than were the voles and disappeared. But during severe spring declines (e.g. Figs 1 and 3 bottom) larger voles did not survive any better, and wounding was significantly more severe in the survivors than it had been in the voles that disappeared. Also during severe declines the survivors were more often captured in breeding condition than were the voles which disappeared. Thus during a spring decline losses were size-selective only when these losses were slight to moderate.

## DISCUSSION

The spring decline is a characteristic feature of the population biology of all small rodents that have been studied and thus may be a phenomenon of general interest. At least six hypotheses have been suggested as applying to the spring decline. These hypotheses are neither mutually exclusive nor exhaustive, and we discuss them here in random order. Most studies of spring declines have been *a posteriori* descriptions of demographic events (as in this paper), and we will now try to analyse these six hypotheses on the basis of past information and to suggest critical experimental tests for the future.

Spring declines could be caused by predation, as implied by Pearson (1966) for *Microtus californicus* (Peale), by Fitzgerald (1977) for *M. montanus* (Peale), and by MacLean, Fitzgerald & Pitelka (1974) and Maher (1970) for *Lemmus sibiricus* (Kerr). This hypothesis can be tested by removing or excluding predators from a population during a spring decline, but no one has yet done this. Boonstra (1977b) measured the rate of predation on one of our populations (grid I) during the spring declines of 1973 and 1974, and predation could account for only 7% of the losses in 1973 and 19% of the losses in 1974. Moreover, during the early part of the breeding season (March–April) almost none of the losses could be traced to predation. We infer that spring declines of *Microtus townsendii* are not caused by predation.

Food shortage at the end of winter could reduce population size, as suggested for *Lemmus sibiricus* by Thompson (1955) and Pitelka (1964), and by Hanson (1971) for *Microtus agrestis* (L.). This hypothesis could be tested by supplying food to a population during late winter and spring. Flowerdew (1972) did this with *Apodemus sylvaticus* (L.) and concluded that excess food nearly eliminated the spring decline in numbers, but his conclusion was somewhat clouded by a month-long gap in supplemental feeding during the middle of one spring decline. Fordham (1971) supplied excess food to a population of *Peromyscus maniculatus* (Wagner) and found that male numbers were not affected but females increased in density.

Spacing behaviour in both sexes might produce spring declines, and many suggestions of this sort appear in the literature (Chitty & Phipps 1966; Petticrew & Sadleir 1974; Krebs, Halpin & Smith 1977; Watts 1969). Experimental evidence, like that available for the red grouse *Lagopus lagopus scoticus* (Watson & Jenkins 1968), is at present available only for *Peromyscus maniculatus* (Sadleir 1965; Healey 1967; Fairbairn 1977). To demonstrate experimentally that spacing behaviour is necessary and sufficient for population

changes is an arduous task (Watson & Moss 1970) and has been achieved for a few species only. We have suggested (Krebs, Redfield & Taitt 1978) that spacing behaviour causes population changes in *Microtus townsendii*, and the data presented in this paper are consistent with this suggestion. However, for voles no one has completed the critical test, which is to manipulate spacing behaviour, although an attempt has been made (Krebs, Halpin & Smith 1977). One difficulty is that spacing behaviour can be affected by environmental variables such as food (Watson & Moss 1970), and the fact that spacing behaviour is involved in spring declines does not exclude other variables.

The suggestion by Fairbairn (1977) that the two sexes might have different causes for spring declines is attractive because it would help explain how the two sexes may be differentially affected in a spring decline (cf. Fig. 1). She suggested that males declined in spring because of dispersal due to spacing behaviour, but females declined because of mortality due to food shortage aggravated by attempting to breed early in spring. We found no evidence for this from spring declines in *M. townsendii*. Male and female voles came into breeding condition during spring declines, and females which began breeding earlier survived better than non-breeding females, the opposite to what Fairbairn (1977) observed. If spacing behaviour causes female losses in voles, it occurs without much evidence of wounding on females. Leuze (1976) has observed agonistic encounters between female water voles *Arvicola terrestris* (Lacépède) at the start of the spring breeding season, and showed that females that lost agonistic encounters all dispersed from the population. In a year of high density 50% of the adult female water voles dispersed after losing agonistic encounters over territories; in a year of low density none of the adult females dispersed. Further detailed work of this sort is badly needed on both male and female voles to uncover the behavioural mechanisms involved in spring declines and possible differences between the two sexes.

Watts (1969) suggested that the spring decline of *Apodemus sylvaticus* populations is density-dependent, and Flowerdew (1972) supports this belief. But the regression test for density-dependence used by Watts (1969) is invalid, and the question of whether *Apodemus* spring declines are density-dependent must be reopened. Similarly, Petticrew & Sadleir (1974) state that the intensity of the spring decline in *Peromyscus maniculatus* is density-dependent, but the data of Fairbairn (1977) do not fit this conclusion. Our data provide no support for the suggestion that the intensity of the decline is related to population density at the start of the decline ( $r=0.4$ ,  $n=18$ ).

Population density is a substitute variable in many demographic analyses, and must be replaced by a primary variable before any experimental programme can be set out. A high population density of voles may mean a reduced food supply, more agonistic interactions, or more exposure to predators, and it is important to specify the causal chain in any statements about 'density-dependence'. For example, the spacing-behaviour model assumes that the intensity of social interaction will vary with population density and with the behavioural phenotypes (aggressive, non-aggressive) comprising the populations. If this is so, we cannot compare a spring decline in one year with one in the next year unless we know that the behaviour of the animals is similar in both years. We should, however, be able to manipulate the intensity of social interaction by changing population density within a single year on an experimental plot. Only a few experiments of this type have been done to investigate the 'density-dependence' hypothesis.

In one of these, Boonstra (1977a) manipulated densities of *Microtus townsendii* populations during and before spring declines. He found that reducing density just at the start of spring breeding did not improve male survival during the spring decline but did improve



female survival. Males seemed programmed to decline regardless of their population level. By contrast, reducing density throughout the previous fall and winter did improve spring survival of both males and females. Survival in spring was not density-dependent in these populations of *M. townsendii*.

The results in Fig. 2 of this paper directly contradict those of Hilborn & Krebs (1976), who marked voles (*M. townsendii*) with radioactive tags in order to determine the fate of disappearing individuals. In one moderate-sized decline Hilborn & Krebs (1976) found little dispersal, but in a severe decline most of the radioactive voles disappeared and presumably dispersed. Either our interpretation of Fig. 2 is incorrect, or conclusions of Hilborn and Krebs are not generally valid for this species. The heavy mortality which seems to occur in severe spring declines (Fig. 2) might occur after emigration. If this were so, the amount of dispersal might be the same in all spring declines, but the immigrants might all be killed in a severe decline. We do not think this interpretation correct because few immigrants colonize vacant areas during severe declines (Krebs *et al.* 1976), and we think that emigration and immigration are both reduced in severe spring declines.

We suspect that spacing behaviour is the primary cause of spring declines in small rodents, but we do not know if it is a sufficient parameter to explain the great variation that we have described in the size of the spring decline. Further progress is likely to come from detailed behavioural analyses of individuals during spring declines, as Leuze (1976) did on *Arvicola terrestris*, and by experiments that alter behaviour with drugs or other chemicals.

The approach used in this paper, describing in detail a set of natural spring declines, is not the best way to determine the casual nexus behind spring declines. Enough detailed descriptions of spring declines are now available for several species of rodents to make the problem ripe for an experimental attack.

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