

THE EFFECT OF EXTRA FOOD ON SMALL RODENT POPULATIONS: II. VOLES (*MICROTUS TOWNSENDII*)

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SUMMARY

(1) Voles on three areas were provided with different levels of extra food in the form of laboratory chow and oats for approximately one year.

(2) On areas with intermediate and high extra food, population density increased to twice the control density.

(3) Extra food increased immigration and reproduction, and shortened the winter non-breeding season.

(4) Males and females had smaller home ranges on areas with extra food. This may have facilitated immigration to these populations.

(5) Voles were removed from three other areas and re-colonization was measured. Immigration was related to the density of extra food; three times as many voles colonized a high food area compared with a control.

(6) These results, combined with those of previous research which has shown that a viable surplus of voles exists in natural populations, suggest that the vole's population size is limited by both behaviour and food.

INTRODUCTION

There is little evidence in microtines for or against limitation of numbers by food. Krebs & Delong (1965) provided extra oats to a low-density vole population for 10 months. Numbers increased for 5 months and then declined over the summer to the low initial density, whereas on the control they continued to increase throughout. However, this experiment has been criticized because oats are not the voles' main food (Watson & Moss 1970; Batzli & Pitelka 1971). In the present study, we did experiments to test for food limitation of numbers in *Microtus townsendii* (Bachman). Specifically, we asked:

(1) Is the number of voles that can be supported in a given area affected by extra food?

(2) Is immigration to a vacated area, and the size of the population that becomes established there, affected by extra food?

METHODS

Study area and trapping technique

Populations of *M. townsendii* were studied on a grassland south of Vancouver in the Fraser River Delta of British Columbia. The grassland had been undisturbed for at least 10 years. In winter the lowest parts are flooded; the 'marsh', in particular, becomes a shallow lake (Fig. 1). The lake remains until April or May depending on rainfall, and then becomes a temporary breeding habitat for voles in summer.

Two sizes of grid were marked out in the grassland. Large grids had 100 trap stations at 7.6 m intervals, usually in a 10×10 checkerboard (0.47 ha). Small grids had 50 traps covering 0.21 ha. The trapping procedure was the same as that used for deer mice (Taitt 1981), except that traps were checked in winter during the intervening day as well as the two overnight periods. In summer, the daytime trapping period was abandoned to avoid mortality from overheating. The type of data recorded on each mouse was identical to that recorded for deer mice.

A: Long-term extra food (grids C, I, L, H)

Grid C (Fig. 1) was the control population trapped by Krebs *et al.* (1976) from May 1971 to September 1975. Grids L and H were set up in July 1972. At the end of March 1973, a high density of food stations (1 per 22 m²) was placed on grid H and a low density on grid L (1 per 73 m²). We had intended to have high and low food available throughout the study on these two grids. Unfortunately ploughing destroyed both in April 1974 after only one year of extra food. In May 1974 we set up grid I and provided it with food stations at an intermediate density (1 per 45 m²) at the end of August 1974. These were removed from grid I 10 weeks before the study ended in September 1975.

B: Colonization and food density (grids 1, 2, 3)

These three small grids were set up on the area ploughed in April 1974. By the end of November 1974, grass was re-growing and some voles were immigrating into the area.

All voles were removed from all grids on 18–20 November. On 25 November, a high density of food stations (1 per 11 m²) was placed on grid 1, a lower density (1 per 33 m²)

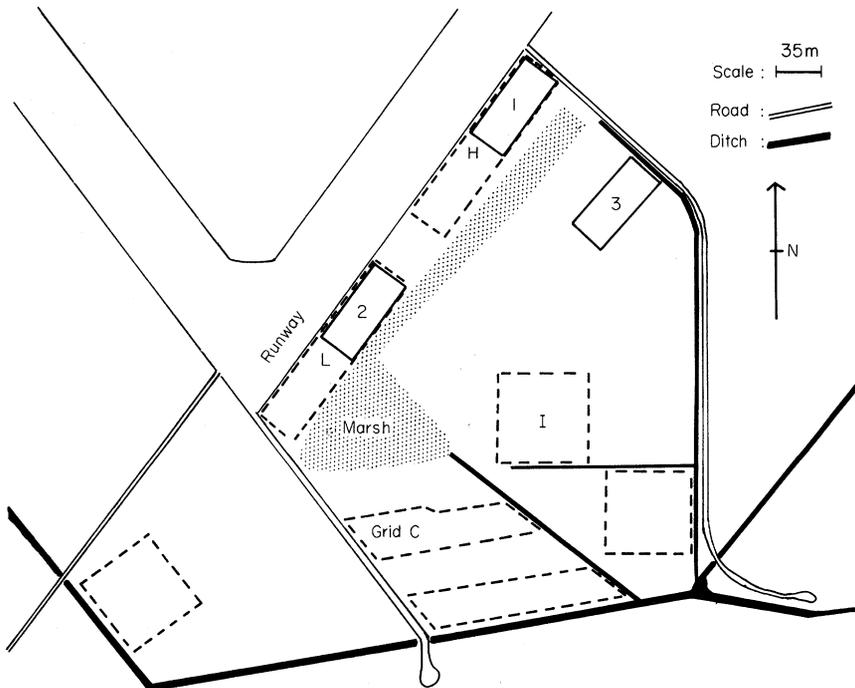


FIG. 1. Location of vole grids at Ladner, B.C. Numbers and letters correspond to those assigned to each grid.

on grid 2, and none on grid 3. After 3 weeks of immigration, all voles were removed in the mid-December trapping period. We reduced the density of food stations on grid 2 to one per 68 m². Voles were then allowed to immigrate freely for the next 4 months to all three grids. Food cans were taken away at the end of April, and all voles removed for the next three trapping sessions.

Food supply

As microtines are herbivores, the most effective method of manipulating their food supply would be to provide them with extra green vegetation or change their vegetation by fertilizers or destruction. However, fertilizers on a large scale over a long period of time would have cost too much, and destruction would have damaged the habitat structure. Further, we wanted to control the distribution of food fairly closely. Following the advice of Dr G. O. Batzli (pers. comm. 1972), we provided voles on grids L and H with a laboratory chow (Purina 5321) for the duration of this experiment. Voles took the chow readily both in the laboratory and from food stations in the field, but it decayed rapidly in wet weather. Since voles took whole oats from live-traps, we used oats mixed with chow on grids I, 1, 2, and 3.

RESULTS

A: Long-term extra food

Trappability

The trappability of voles on the control C and experimental grids (L, H, I) was calculated as described for deermice (Taitt 1981). The voles were more trappable than the deermice at similar densities, and trappability averaged 70% during the study. It declined progressively as the number of voles increased (Taitt 1978), but never fell below 50% in any 3-month period. Thus our population estimates should have a maximum error of 10% (Hilborn, Redfield & Krebs 1976).

Population density

The density of voles on the control grid C was very low when the grid was first established in June 1971 (see Krebs *et al.* 1976). From an early winter (November) peak of 27 voles the population declined to 12 in March 1972. When grids L and H were established in July 1972, numbers on the control were increasing towards its second winter peak of 58 voles (Fig. 2). The populations on grids L and H increased rapidly at the end of October. The reason for this increase was that voles in the area that became a winter 'lake' emigrated to slightly higher ground along the edge of the runway where the two experimental grids were positioned (Fig. 1) Over the three months (January to March), the control declined at an average of 1% per week, while grid L continued to increase at 2% per week and grid H at 4% per week.

The number of voles on grids L and H continued to increase after food was added on 18 March 1973 (Fig. 2). We compared the ratios of population sizes on experimental/control areas before and after food addition. Data were pooled over 3-month periods and a *t*-test made on the before-after ratios. Both the low and high food treatments significantly increased population size ($P < 0.05$). Density on the high food grid was 2.06 times that on the control before treatment, but 3.68 times after treatment. The low food grid had 1.57 times the control density before the treatment, but 2.03 times after it.

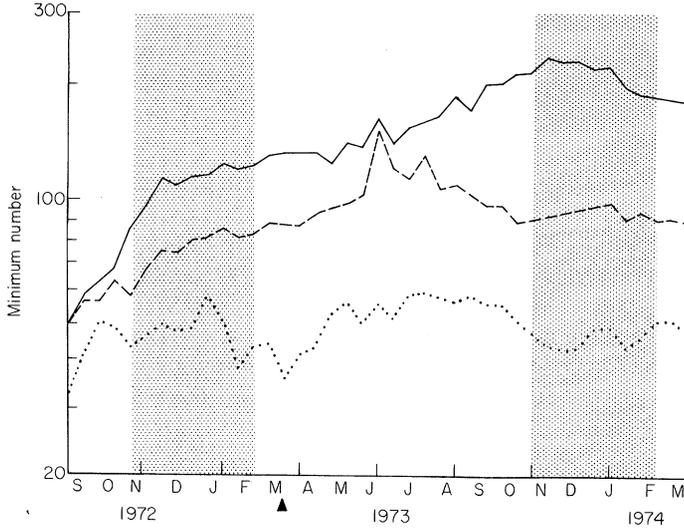


FIG. 2. Number of voles on grids C, L, and H. Winter months are shaded ... grid C (control); --- grid L (low food); — grid H (high food); ▲, food added to grids L and H.

After the destruction of the two experimental areas in April 1974, we began a second feeding experiment on adjacent grid I (see Fig. 1). The density of voles on grid I was close to that of the control (Fig. 3) at the end of August 1974, when an intermediate density of food stations was added. The number of voles on both grids increased rapidly (control 7%, intermediate-food 10% per week) over the next four months. The population increase on food grid I differed between the sexes; females increased faster than males. The control

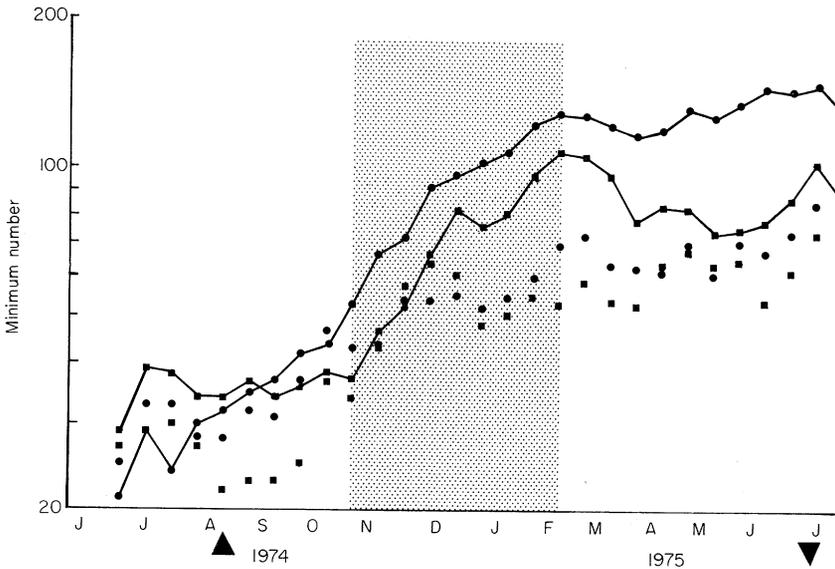


FIG. 3. Number of male and female voles on grids. Control (unjoined points) and intermediate food (joined points). ■, males; ●, females; ▲, food added to grid I; ▼, food removed.

population remained fairly stable over the early summer, and then increased again towards the end of the study in autumn 1975. The intermediate-food population diverged from the control in December and increased to double its number by March. Both sexes contributed equally to this increase. Over the next three months male density declined, while females increased still further with intermediate food.

Immigration and survival

The total number of new voles caught on all grids in each 3-month period is shown in Table 1. Grids L and H had more new voles than the control in the nine months before food was provided. During summer 1974, following food addition, the number of new voles on the low food grid (L) rose to 1.9 times that on the control, and on the high-food grid (H) to 2.5 times. The low-food population had almost the same number of new voles as the control over the 1973/4 winter, but the high food grid had 2.9 times the number on the control. The number of new voles caught on the intermediate-food grid (I) was 1.7 times that on the control area overwinter (1974/5) and twice that on the control over the summer of 1975.

During the year when food was added to grids L and H, more of the new voles on the control were males (106:70). Males also predominated (181:152) amongst immigrants to the control over the nine months of intermediate food addition to grid I. The number of males amongst new voles on each food grid, in order of food level from low to high, was: 1.5 times, 1.8 times, and 2.2 times the number on the control. Similarly, new females on each food grid in order were: 1.7 times, 2.3 times, and 3.1 times those on the control. Therefore, both sexes recruited to food grids in proportion to the food available, but females more so than males.

In terms of the sex composition of each age class, immigrants to all vole populations showed the same general pattern as deer mice. The sex ratio in the sub-adult category was close to even. Females predominated in the juvenile age class, while new adults in all populations were predominantly males (Taitt 1978).

TABLE 1. Number of new voles caught on grids C, L, H, and I

Period	Grid C	Grid L	Grid H	Grid I
1972				
July–Sept.	84	90	93	–
Oct.–Dec.	44	60	96	–
1973				
Jan.–March	28	44*	73*	–
April–June	66	126	134	–
July–Sept.	52	92	156	–
Oct.–Dec.	24	30	99	–
1974				
Jan.–March	34	39	69	–
April–June	92	–	–	–
July–Sept.	68	–	–	113*
Oct.–Dec.	134	–	–	193
1975				
Jan.–March	101	–	–	215
April–June	108	–	–	268
July–Sept.	196	–	–	347

* Extra food provided from this point onwards.

TABLE 2. Survival of voles on grids C, L, H, and I, with sample size in parentheses. None of these differences is significant except for the grid C-grid I comparison

Grid	July 1972-March 1973 (before food)		July 1973-March 1974 (with food)	
	Males	Females	Males	Females
C	0.88 (195)	0.88 (104)	0.84 (228)	0.87 (145)
L	0.91 (301)	0.90 (189)	0.84 (296)	0.86 (150)
H	0.90 (395)	0.94 (324)	0.89 (614)	0.90 (571)
	October 1974-June 1975 (with food)			
C	0.83 (689)	0.92 (671)		
I	0.72 (652)	0.82 (756)		

C = control; L = low food; H = high food, I = intermediate food.

In the nine months before food was added, adult vole survival on grids L and H was not significantly higher than on the control (Table 2). The addition of supplemental food to both experimental grids (L, H) did not change survival. On grid I, however, with an intermediate level of food from October 1974 to June 1975, adults of both sexes survived worse than on the control. This was particularly marked in the two months following food removal, when adult male survival declined to 0.52 and female survival to 0.59 compared with 0.72 and 0.82 respectively on the control. Before food was added, juveniles on both experimental grids (L, and H) survived better than on the control (Table 3). In the six months after food addition, the number of lactating females on both food grids was equal and amounted to more than twice that on the control. Juveniles survived worse than on the control at this time. However, in the fall and winter 1973/4, when the number of lactating females became similar on all three grids, survival rates were slightly higher on the food

TABLE 3. Survival rate per 2 weeks of juvenile and subadult voles, and number of lactating females, averaged over 3-month intervals. Extra food was added to grids L and H in April 1973. Sample sizes in parentheses

Time	Grid C (Control)		Grid L (Low food)		Grid H (High food)	
	Survival	Lactating females	Survival	Lactating females	Survival	Lactating females
1972						
July-Sept.	0.77 (65)	2.5	0.83 (93)	2.7	0.76 (76)	1.5
Oct.-Dec.	0.83 (173)	1.5	0.87 (211)	3.0	0.90 (254)	2.3
1973						
Jan.-March	0.83 (167)	1.9	0.94 (266)	6.1	0.93 (311)	4.7
April-June	0.72 (47)	5.0	0.63 (52)	15.0	0.72 (76)	15.8
July-Sept.	0.86 (108)	4.8	0.79 (358)	11.9	0.78 (305)	11.6
Oct.-Dec.	0.87 (147)	2.3	0.94 (421)	0.2	0.92 (540)	4.3
1974						
Jan.-March	0.91 (196)	0.1	0.93 (342)	0.6	0.87 (373)	1.3
	Grid C (Control)		Grid I (Intermediate food)			
1974						
Oct.-Dec.	0.84 (205)	4.6	0.74 (141)	10.7		
1975						
Jan.-March	0.79 (122)	11.5	0.68 (217)	12.7		
April-June	0.55 (38)	28.3	0.31 (109)	37.2		
July-Sept.	0.72 (124)	8.0	0.39 (299)	25.0		

TABLE 4. Mean home range size (m²) of voles on grids C, L, H, and I, with sample size in parentheses. Periods are July to March in each year

		1972/3	1973/4	1974/5
Grid C	Males	804 (42)	1134 (51)	670 (85)
	Females	546 (45)	608 (38)	391 (79)
Grid L	Males	1050 (50)	445 (79)‡	—
	Females	578 (65)	331 (78)‡	—
Grid H	Males	795 (74)	328 (102)*	—
	Females	423 (89)	261 (114)*	—
Grid I	Males	—	—	447 (87)†
	Females	—	—	231 (92)†

* High food.

† Intermediate food.

‡ Low food.

grids. In the spring and summer of 1975, the number of lactating females on grid I with intermediate food was higher than on the control, and juvenile survival was much worse.

Home range size

Home ranges of voles were calculated as described for deermice (Koepl, Slade & Hoffmann 1975). Home ranges were calculated for blocks of data: the nine months before food was added to grids L and H (July 1972 to March 1973), the same time period a year later when grids L and H were receiving extra food, and the following year, when food was added to grid I (Table 4). In the first year (1972/3) size of home ranges of both sexes did not differ significantly between control and experimental grids. During the period of food addition, however, both males and females on grid L and grid H had significantly smaller home ranges than males on the control ($P < 0.01$ for all comparisons). With an intermediate level of food (grid I) both sexes had significantly smaller home ranges than controls (males: $t = 2.63$, $P < 0.01$; females: $t = 3.33$, $P < 0.001$). Females had smaller home ranges than males in all periods on all grids.

Breeding season

Voies in the control area bred nearly continuously throughout the study. This made it difficult to observe the influence of additional food on breeding activity. Before food was added to grids L and H, male voies on all grids were breeding. In the following winter, males on the control had stopped breeding by the end of December 1973. On grid L, which had a higher density of voies and a low level of extra food, males had gone out of breeding condition in November, some 6 weeks earlier than on the control. But with a high level of food, males on grid H continued to breed. In fact they stopped breeding for only 6 weeks in mid-winter on grid H, compared with 12 weeks on grid L and 10 weeks on the control (Taitt 1978).

Females with extra food showed no appreciable increase in breeding intensity, but the period of non-breeding was shorter on the high-food area. On grid L, with a low density of food but with twice the density of voies compared with the control, females ceased breeding for 26 weeks in the winter of 1973–74, as compared with 18 weeks on the control. Females in the high-density population with a high level of food (H) did not breed for 12 weeks.

Apart from one trapping period at the end of August 1975, males and females bred continuously on the control from spring 1974 until the study ended. More than 50% of the

males were scrotal on the intermediate-food grid in February 1975, 6 weeks ahead of the control males. More females were lactating on the intermediate-food area compared with control females in 1975. After the removal of food stations at the beginning of July 1975, male reproduction dropped below 50% 2 weeks later and female breeding ceased completely, while both sexes on the control continued at their summer intensity (Taitt 1978).

Breeding success

Reproductive output, in terms of the number of young recruited, varied widely on the control. For example, in the 3-month period from October to December, 34 young were recruited in 1972, 23 in 1973, and 88 in 1974. Before food was added to grids L and H, 76 young had been recruited to the control grid. The number recruited to grid L was 1.4 times higher (113) and to grid H 1.9 times higher (148) than the number to the control. Over the six months following food addition, 59 young were recruited to the control (C). The low-food population had 163 young (2.8 times that on grid C), and the high-food grid 215 young (3.6 times that on grid C) over this period. Therefore the number of young entering the food grids was twice that before food was added. Before food addition to grid I, the number of young voles present was similar to the number on the control. During the next 9 months, however, over twice as many young (337) were recruited to the intermediate-food population as to the control (159).

Weights and growth

There was a strong annual cycle in mean weight on all grids (Fig. 4), the lowest in early to mid-winter and the highest in late spring. After the addition of food to grids L and H in 1973, the mean weight in these populations became significantly higher than that on the

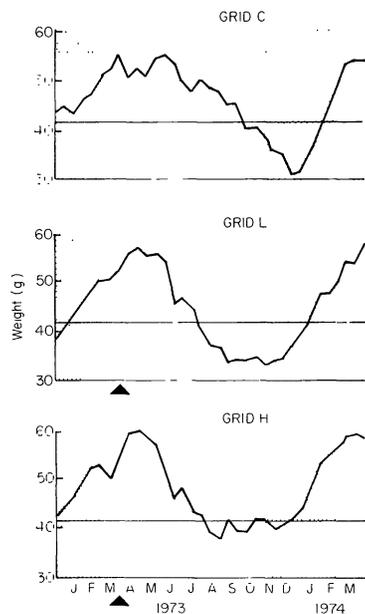


FIG. 4. Mean weights of voles on grids C (control), L (low food) and H (high food). ▲, food added to grids L and H.

TABLE 5. Instantaneous relative growth rates of male voles adjusted to a standard body weight of 38.5 g, with sample sizes in parentheses

	Dec.–March 1973 (before food)	April–July 1973	Aug.–Nov. 1973 (after food)	Dec.–March 1974
Control (Grid C)	0.0065 (68)	0.0085 (49)	−0.0003 (116)	0.0057 (120)
Low food (Grid L)	0.0061 (127)	0.0025 (63)	−0.0010 (287)	0.0052 (184)
High food (Grid H)	0.0066 (134)	0.0110 (40)	0.0011 (256)	0.0047 (191)

control by the following trapping period ($P < 0.05$). On grid H, with the highest level of food, the mean weight was significantly higher than on both grid L and the control. The lowest winter weights on the control were smaller than those on the low-food grid, which in turn were smaller than those on the high-food grid. In fact, voles on grid H maintained higher mean weights than did the controls from the end of November 1973 till the destruction of the grid in April 1974.

We had expected growth rates to increase when we added food. We tested this by an analysis of covariance on the instantaneous growth rates of male voles below 50 g, with body weight as a covariate. There was a significant interaction between treatment and time periods, but a Duncan's multiple range test showed extensive overlap in treatment effects. Growth rates were equal on all grids before food addition. After food was added, growth rates on the high food grid exceeded those on both the low food grid and the control, especially in the 20–40 g weight classes. High food thus improved growth up to the autumn of 1973 (Table 5). Through the winter 1973 and spring 1974, growth rates were similar for both food treatments and the control. We suggest that the high densities reached on grids L and H counteracted the presence of extra food, such that body growth was no longer enhanced.

B: Colonization and food density

Population density

In this experiment we measured the colonization of voles on areas that had different densities of food stations. A similar number of voles was removed from all three grids before food was added in November 1974, and also after the first week of food addition (Fig. 5). However, over the second and third week of food addition to grids 1 and 2, the number of new voles was in proportion to the amount of extra food available.

Over the 4-month colonization period, the population with a high level of food increased at an average of 50% per week compared with 30 and 35% respectively on the low-food grid and the control. After the three removal periods in April and May 1975, the total number of voles (males: females) that had colonized the high-food grid was 188 (97:91), compared with 116 (62:54) on the low-food grid, and only 53 (16:37) on the control. Therefore, three times as many voles colonized an area with high food compared with one with no extra food. Twice as many colonized an area with low food compared with one with no extra food.

This experiment was repeated in June and July 1975 (Fig. 5) with the treatments reversed. We observed over this short period a repetition of the pattern in the first experiment.

Immigrants

The data on immigrants (new voles caught in each trapping period) reflected two previous trends found for voles (and deer mice) in this study. First, the total number of

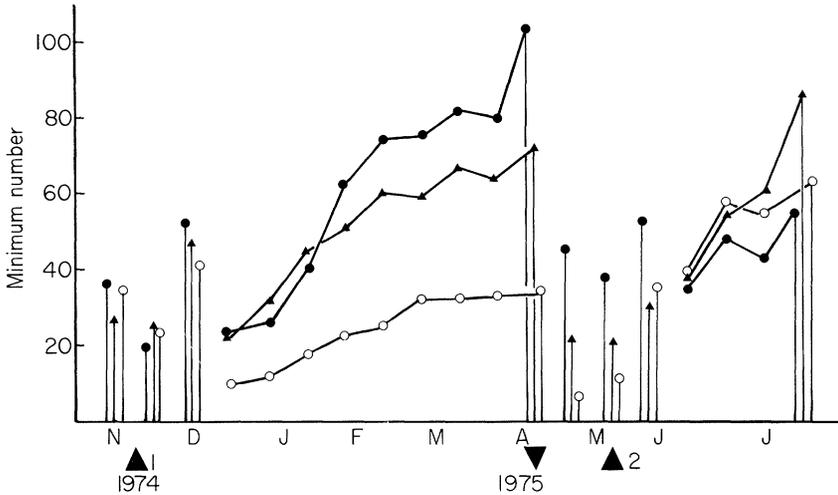


Fig. 5. Number of voles on grids 1, 2, and 3. Vertical lines show the number of voles removed. ●, grid 1 (high food then no food); ▲, grid 2 (low food then high food); ○, grid 3 (no food then low food); ▲1, high food to grid 1 and low to grid 2; ▼, food removed; ▲2, high food to grid 2 and low to grid 3.

immigrants was proportional to the extra food available (Jan. to May 1975: high food 241, low food 136, no food 77; June to July 1975: high food 153, low food 140, no food 106). Second, adult immigrants were predominantly males (283:210), and juveniles were predominantly females (42:70), while subadult immigrants had a close to even sex-ratio (114:134).

DISCUSSION

Before food was added, the density of voles on experimental grids L and H had increased above that of the control; this was probably in response to winter flooding of the marsh bordering grids L and H (Fig. 1). In retrospect, we should have delayed adding food until the lake had dried out in the summer of 1973, because some voles might have left both areas (L and H) to colonize the new habitat, and hence the densities on these grids might have been closer to that on the control (C). However, after 1 year of low-extra food, the grid L population still had twice the number of voles as on the control (C). The grid H population reached 4.2 times the control density after one year of high-food compared with its pre-food density of 2.8 times that on the control. After 9 months of intermediate food, grid I had double the control density of voles, although both had the same density prior to food addition.

Voles immigrated into experimental populations in proportion to the extra food provided. This may have been facilitated by males and females reducing the size of their home ranges on food grids compared with those of voles on the control areas. Colonization of vacant areas provided with different levels of food confirmed the observations for the long-term food grids. Populations were largest on areas with most extra food.

It was difficult to detect the influence of food availability on the breeding season, partly because breeding was almost continuous on the controls. The non-breeding season was shorter in a population with a high level of food compared with one with no extra food.

Also more male and female voles bred on areas with extra food, and more young were recruited to populations with extra food compared with controls.

The effect of extra food on numbers has been reported on two other vole species. Flowerdew (1973) fed bank voles (*Clethrionomys glareolus*) with wheat for 16 months in England. As in the present study, he found no significant change in breeding season. However, Andrzejewski (1975) in Poland found that 90% of female bank voles were breeding in early spring on a plot with high oat-food, compared with 53% on a low-food area and only 23% on a control plot. Both studies reported little change in survival of voles on the food plots. Andrzejewski (1975) found a large increase in immigration to his food plots, but Flowerdew (1973) noted an increase one year but none the next year. In a later short-term experiment, Flowerdew (1976) concluded that this equivocal response resulted from bank voles not significantly changing their distribution in response to the extra food. However, in another such experiment with bank voles, Andrzejewski & Mazurkiewicz (1976) found that voles in an island population had smaller home ranges than they had had in previous years without food. Finally, Cole & Batzli (1978) fed laboratory chow to a population of prairie voles (*M. ochrogaster*) for just over a year, and densities on the food grid reached 50% higher than the control.

These equivocal results may be a consequence of the type of extra food provided. If voles prefer green plant food, as suggested by Batzli (1974), or require it to reproduce, as suggested by Negus & Berger (1977), then the only effective way of manipulating their food supply will be to alter the food plants by fertilizers or destruction.

Dynamics of mice and voles

Granivorous rodents have larger home ranges than herbivorous ones (McNab 1963). However, in the presence of extra food, both mice (Taitt 1981) and voles reduced their home ranges. In fact, female deermice had ranges the size of non-fed male voles. This confirms McNab's (1963) suggestion that the difference in home-range size of granivores and herbivores may be a result of the distribution of food.

Does the distribution of food in the 'typical' habitats of these two rodent types affect the population dynamics observed? Taitt (1981) suggested that deermice survive the winter restriction of their food supply in the forest by ceasing to breed, and hence show an annual cycle in numbers. By contrast, food on homogeneous grasslands is far less restricted in time and space, especially for low-density vole populations. Cyclic vole populations typically breed through the first winter (Krebs & Myers 1974). Further, Taitt (1981) showed that deermice will also breed overwinter in the forest if extra food is made available. Also a population of *M. pennsylvanicus* in woodland ceased breeding in winter, when a nearby grassland population did breed (Grant 1975). Perhaps cyclic vole populations would show an annual cycle if food supply could be reduced in time and space. Grassland populations of *M. townsendii* which do not appear to be typically cyclic (Krebs 1979) may be a case in point. Temporal and spatial heterogeneity is imposed by the winter flooding of patches of these low-altitude grasslands. In summer, such patches are good habitat and voles disperse into them and breed. In winter, however, voles have to leave for patches of higher ground, which, because of the high water-table, are not high enough to allow deep burrows. The increased density may, through increased interaction as suggested for deermice (Taitt 1981), cause a decline in weight and halt reproduction. The net result is that populations rise to an annual peak density in winter.

Another difference between these rodents is that the food supply of voles is also their cover, protecting them from predators. A cyclic vole population may not reduce the cover

until they reach peak densities, and thus they could escape predation for as much as two years. At peak density they can reduce their main food plants by as much as 85% (Batzli & Pitelka 1970). By contrast, patches of low-altitude grasslands inhabited by *M. townsendii* may be protected from such overexploitation by winter flooding. Further, high winter densities may reduce cover in non-flooded patches. If subordinate voles are excluded in spring as in deermice, these can easily be removed by avian predators from such low-cover patches. This is quite likely since small voles tend to be subordinates (Turner & Iverson 1973), and Beacham (1979) has shown that avian predators select small *M. townsendii*. Thus, the patchwork of favourable and temporally unfavourable habitat, the movement of individuals between such patches, and the removal of subordinates by predation in spring may provide enough habitat heterogeneity so that this vole species can show an annual cycle of numbers like the deermouse. This explanation for the absence of population cycles in *M. townsendii* is an alternative to the genetical hypothesis suggested by Krebs (1979).

Spacing behaviour and population regulation

The colonization of new areas from which resident *P. maniculatus* and *M. townsendii* have been removed indicates that a surplus exists in populations of both species. Further, pulsed-removal experiments on both species show that these surplus animals are capable of breeding (references in Taitt 1981). Thus conditions A and B of the Watson & Moss model (1970) are fulfilled indicating that spacing behaviour limits population size in these species. However, the results of feeding experiments show that resident mice (Taitt 1981) and voles change their spacing behaviour (measured as home ranges) following experimental changes in food. Deermice reached a maximum density of 82 mice/ha with extra food compared with 33/ha on the control. Voles reached a peak of 734/ha with high food, 504/ha with intermediate food and 209/ha with low food. Thus condition E of the Watson & Moss model (1970) is also fulfilled, this indicates that both food and behaviour limit population size in these rodent species. The present study suggests that the availability of other environmental resources and individual differences in resource requirements would be worth examining in future work. For example, lactating rodents may space themselves in relation to food and nest sites, whereas males may space themselves in relation to oestrous females and cover. Hence both would exclude a different sub-set of the population by their behaviour.

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