

PREDATION, COVER, AND FOOD MANIPULATIONS DURING A SPRING DECLINE OF *MICROTUS* *TOWNSENDII*

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SUMMARY

(1) We manipulated, in combination, predation, cover, and food for populations of *Microtus townsendii* during spring 1981.

(2) We suspended fish net over grassland to reduce heron predation, cut the grass to increase predation and decrease cover, spread straw to increase cover, and provided whole oats as extra food.

(3) In the first 6 weeks of spring, high precipitation caused flooding, natural cover was poor, and peak numbers of herons were present. In the following 4 weeks there was no flooding, natural vegetation was improving, and few predators were present.

(4) Populations protected from predation had higher immigration, survival, and density than unprotected populations in the 6-week period, while populations with extra cover and food increased in number. Voles with food were heavier and reproduced earlier than voles on all other grids.

(5) All populations, irrespective of treatment, exhibited compensatory loss in the later 4-week period. In this period, males moved more and had more wounds, while females were lactating and had shorter movements than in the early spring.

(6) We conclude that the first 6-week period of the 1981 spring decline was the result of predation, and the last 4-weeks of the decline was the result of density-dependent dispersal, possibly induced by interactions with mature females.

INTRODUCTION

A substantial decline in population density in spring is associated with some rodent populations that exhibit annual fluctuations in numbers (*Peromyscus maniculatus* (Wagner), Sadleir 1965; *Microtus breweri* (Baird), Tamarin 1977; *M. townsendii* (Bachman), Taitt *et al.* (1981). On the other hand, little or no spring decline in density, particularly of females, occurs in microtine species that undergo multi-annual population cycles (*M. pennsylvanicus* (Ord), Tamarin 1977; *M. townsendii*, Krebs 1979; Beacham 1980). Long-term data for *M. townsendii* show that populations of this species exhibit both annual fluctuations and cycles in numbers. Furthermore, these population patterns were preceded by the expected form of spring decline (Taitt *et al.* 1981).

Experimental manipulations of male and female behaviour in populations of *M. townsendii* were disappointing in not producing substantial changes in spring population dynamics (Gipps *et al.* 1981; Taitt & Krebs 1982). On the other hand, a preliminary

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attempt at manipulating an extrinsic variable was more successful (Taitt *et al.* 1981); when straw cover was added in spring, male vole density declined less than male density in a control population, while female density increased. This result and the possibility of manipulating the form of the spring decline—and hence, perhaps, the form of the population fluctuation—lead us to the present experiments in which we have attempted to manipulate predation pressure, cover and food in *M. townsendii* populations.

METHODS AND EXPERIMENTS

Six trapping grids were established in grassland on Westham Island in the Fraser River Delta south of Vancouver, B.C. Canada (Fig. 1). All grids except grid 1 were bounded on one side by a 6 mm (1/4") wire-mesh fence, and, on the side at right angles, by either a road (grids 2 and 3) or a water-filled ditch (grids 4, 5, and 6). Grid 1 was bounded on one side by a road and on the other by a water-filled ditch. We used this grid design to reduce edge effects and swamping of our populations by immigrants.

Two Longworth live-traps were placed at each of thirty-nine points 7.6 m apart on each grid. Voles were trapped every 2 weeks for two nights and the intervening day from November to May. Traps were locked open for prebaiting between trapping periods. Each new vole captured was given a numbered ear tag and its location, weight, and breeding condition were recorded. Males had either abdominal or scrotal testes; females had open or closed vaginas and small, medium or large nipples. All pregnancies and trap litters were noted. Voles weighing <30 g were classed as juveniles, sub-adults weighed 30–42 g and all voles >42 g were adults. All wounds on the rear of each vole were counted.

The extrinsic factors over which we had no control, but which may have been important, were the invasion of Canada thistle (*Cirsium arvensis*, L. Scop.), and unusually heavy precipitation. Since studies began in this grassland in 1972 (LeDuc & Krebs 1975), increasing numbers of thistles have invaded; this has resulted in declining grass cover because thistles compete with grasses in summer, then die back completely in winter. Heavy rain (Appendix 1) resulted in a high water table and continuous flooding of parts of some grids from November 1980 to February 1981.

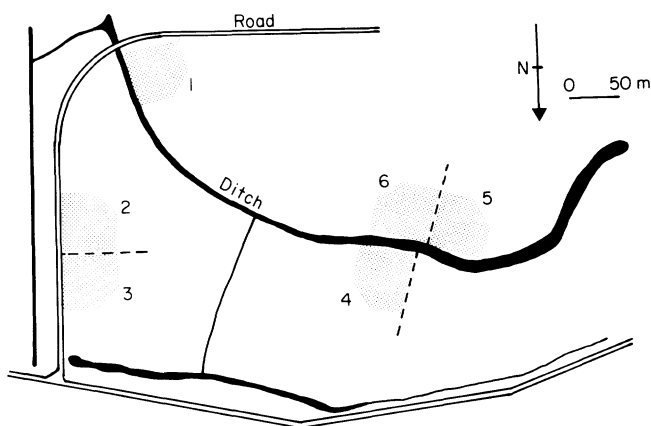


FIG. 1. Location of the grid populations on Westham Island, British Columbia.

We summarize the combination of experimental treatments in Table 1. Manipulations began in February and were completed by the end of the month. We put fish net over grids 1, 4, 5 and 6 to stop predation by the great blue heron (*Ardea herodias*, L.). Cover was reduced by mowing grid 2 and grid 5, and increased by spreading straw on grids 1 and 6. Extra food (whole oats) was provided in feeding stations at every trap station on grid 1.

The number of herons and their location was recorded on each visit to the grids. We photographed grids once a month in 1980/81 and 1981/82, and in 1981/82 we measured cover. A 7 cm length of 1.5 cm diameter wooden post was driven into the ground at thirty evenly-spaced locations on each grid. The end of the post was exposed 1 cm above the soil surface, and the end painted yellow. A cover reading was made every trapping session by standing over the post and estimating to the nearest quarter how much of the yellow disc was visible.

TABLE 1. Summary of experimental treatment of each grid from February to May 1981

Grid number	Treatment
Grid 3	Control
Grid 2	Reduced cover
Grid 4	Net
Grid 5	Net - Cover
Grid 6	Net + Cover
Grid 1	Net + Cover + Food

RESULTS

Predators and cover

The average number of herons observed hunting in the grassland in each trapping period is plotted in Fig. 2. The highest numbers were seen in late February. The number then declined, except in one period in April which was coincident with a record high rainfall (Appendix 1). Observations of herons hunting in the grassland indicated that they could capture an average of three voles in an hour. The number of herons seen on each grid indicates that our experimental attempts to increase (grid 2) and reduce (grids 1, 4, 5, and 6) predation were successful (Table 2).

We have cover measurements for 1981/82 only (Fig. 2). All grids had 50% or less cover at the end of January 1982. Grids with straw had improved cover while other grids had low cover into March. Then natural cover improved on all grids as the grass started to grow. Photographs indicate that the cover pattern was similar in both years.

Reproduction

The spring decline can be divided into two periods. The first period is 6 weeks from early February to mid-March. This period is referred to as the 'onset', because some voles began breeding but, in the first 4 weeks, less than 30% of the males had descended testes, and no more than one female was lactating per grid, except for the grid with extra food (1) (Table 3). The second period (mid-March to mid-April) is the 'true' breeding period, when over 40% of males had scrotal testes at the beginning of the period, and increasing numbers of females were lactating.

The maximum number of males with scrotal testes on grids without netting (Control and reduced cover) was not reached until late April (Table 3). Grids with netting had more

Predation cover and food for voles

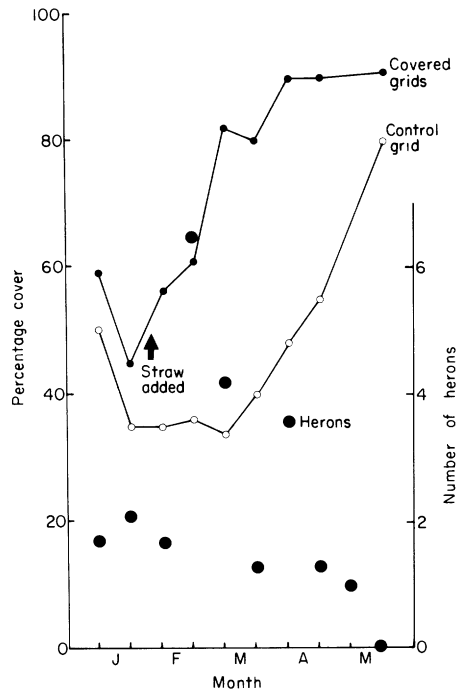


FIG. 2. The average number of herons seen per visit to the grids in each trapping period in 1981, and mean cover measures for grids with and without extra cover in 1982.

TABLE 2. The total number of herons seen on each grid during the 'onset' and 'true' breeding periods in 1981

Grids	February to mid-March	mid-March to mid-April
Control (3)	21	12
Reduced cover (2)	31	10
Net + Reduced cover (5)	3	5
Net (4)	5	5
Net + Cover (6)	6	3
Net + Cover + Food (1)	1	3

reproductive males and they were recorded 4–6 weeks earlier than on the non-netted grids. The number of breeding males on grids with netting then declined to close to the control level; the largest decline occurred on the grid with reduced cover (5) and the smallest decline on the grid with extra food and cover in addition to the netting (1).

The number of females with perforate vaginas was similar on all grids up to early March. But more females were perforate on all manipulated grids compared to the control by mid-March (Table 3). The average number of perforate females on the control from mid-March to early May was 15, while the grids with reduced cover (2 and 5) had 7.5 more perforate females than the control. The netted grid and net + cover grid (4 and 6) had twice as many as the control, while there was an average of 37.5 perforate females on the extra food grid (1). However, if we consider the average number of lactating females, grids were more similar than expected. An average of thirteen females were lactating on the

TABLE 3. The breeding condition of voles during spring 1981; the number (%) of males with scrotal testes, and number of females with perforate vaginas (P) and lactating (L)

Date in 1981	Control (3)			Reduced Cover (2)			Net - Cover (5)		
	♂	P	L	♂	P	L	♂	P	L
2-6 Feb.	1 (2)	16	0	0	9	0	1 (2)	15	0
16-20 Feb.	4 (12)	12	1	2 (7)	17	1	2 (5)	7	1
2-6 March	8 (27)	19	0	7 (27)	23	1	4 (10)	19	0
16-20 March	13 (42)	15	5	12 (46)	26	4	28 (62)	27	1
30 March-3 April	13 (52)	15	16	14 (61)	22	4	18 (58)	20	8
13-17 April	15 (83)	15	16	17 (94)	22	18	12 (86)	17	7
27 April-1 May	18 (95)	15	15	21 (100)	18	22	14 (100)	28	26
	Net (4)			Net + Cover (6)			Net + Cover + Food (1)		
	♂	P	L	♂	P	L	♂	P	L
2-6 Feb.	0	11	0	1 (2)	17	0	0	16	0
16-20 Feb.	0	3	1	2 (4)	19	1	6 (13)	28	2
2-6 March	6 (11)	21	0	6 (12)	15	1	16 (29)	26	9
16-20 March	28 (60)	28	5	19 (38)	39	4	35 (69)	34	22
30 March-3 April	19 (61)	32	14	26 (69)	29	6	23 (74)	35	26
13-17 April	15 (88)	39	9	12 (57)	24	7	15 (52)	39	14
26 April-1 May	23 (100)	30	39	22 (92)	21	31	30 (77)	42	21

control, which was similar to all other grids except the food grid (1), where an average of twenty-one females were lactating (Table 3). This indicates that the number of females maturing may have been restricted (Bujalska 1973; Saitoh 1961).

Population size

The minimum number of voles alive on each grid in 1980/81 is shown in Fig. 3. A marked decline in male density occurred on the reduced cover grid (2) and the control (3) during the 'onset' period. This is in contrast to the pattern on all grids with netting which maintained similar high numbers of males until mid-March. The addition of cover (grids 1 and 6) resulted in an increase in male numbers during the 'onset' period with the largest increase recorded where both cover and food were added (1). Males on all grids declined dramatically during the first month of the 'true' breeding period, except those with extra cover plus food (1).

Female voles have a different pattern of population dynamics from males. In the 'onset' period females either maintained their density without netting (grids 2 and 3) or increased in density with netting (grids 1, 4, 5, 6). During the 'true' breeding period, female density declined on all grids, except the grid with extra cover and food (1) where numbers nearly doubled then declined.

Immigration and births

More new voles were captured on grids with netting (1, 4, 5, 6) than grids without netting (2, 3) during the 'onset' period (Table 4). Immigration was highest to the grids that had extra cover in addition to netting (1, 6) in this period.

The number of new voles on all grids without extra cover (2, 3, 4, 5) was similar irrespective of the presence of netting (4, 5) during the 'true' period. We captured 2.5 times as many new voles in areas with extra cover (6) compared with the control, and ten times as many on grid 1 with extra food in addition to cover. The high level of immigration to the

Predation cover and food for voles

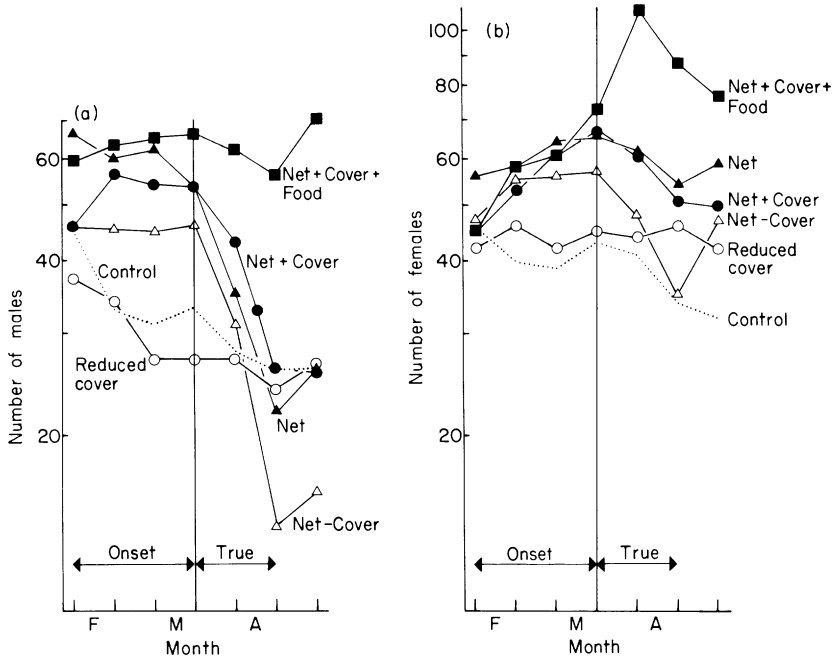


FIG. 3. The minimum number of (a) male and (b) female voles on each grid in 1981: ■ = grid 1 (net + cover + food); ○ = grid 2 (reduced cover); ● = grid 3 (control); ▲ = grid 4 (net); △ = grid 5 (net - cover); ● = grid 6 (net + cover).

TABLE 4. Number of new voles captured on each grid during the 'onset' and 'true' breeding periods. Ad = adults, Sa + Juv = sub-adults and juveniles.

Grids		'Onset' (2 Feb.-20 March)			'True' (20 March-17 April)		
		♂	♀	total	♂	♀	total
Control (3)	Ad	10	5	10:8	4	1	10:4
	Sa + Juv	0	3		6	3	
Reduced cover (2)	Ad	14	16	15:22	4	3	7:10
	Sa + Juv	1	6		3	7	
Net - Cover (5)	Ad	23	21	23:21	8	5	8:6
	Sa + Juv	0	0		0	1	
Net (4)	Ad	20	22	21:28	2	5	4:8
	Sa + Juv	1	6		2	3	
Net + Cover (6)	Ad	42	33	43:34	10	12	16:18
	Sa + Juv	1	1		6	6	
Net + Cover + Food (1)	Ad	21	29	31:37	10	16	57:86
	Sa + Juv	10	8		47	70	

grid with extra cover and food (1) during the 'true' breeding period was the result of early reproduction. Thirteen times as many sub-adults and juveniles were captured on this grid (1) compared to the average on the control.

The sex ratio of immigrants was not different from even in any period on any grid except grid 1. Significantly more females were captured on this grid with extra cover and food during the 'true' breeding period (chi square = 5.88, $P < 0.02$).

Death and emigration

We have calculated the survival of all voles that were captured at least twice in each population (Table 5). Females had higher survival than males on all grids in both periods. Males and females on areas with reduced cover (2) had lower survival than males and females on all other grids during the 'onset' period. We recorded the highest survival on the grids with extra cover (1 and 6) in this period. However, these trends were reversed during the 'true' breeding period when survival was poorer on the grids with the highest vole densities, irrespective of experimental treatment.

New habitat became available in the 'true' breeding period because previously flooded areas had dried up and cover in them was now as good as in the previously unflooded areas. We suggest therefore, that most of the voles that disappeared in the 'true' period were immigrants. The number disappearing was correlated ($r = 0.93$) with the density of voles on each grid (Fig. 4). It was more closely correlated with female density ($t = 0.93$) than male density ($r = 0.83$).

TABLE 5. Average survival of voles caught at least twice. The percentage surviving/2 weeks is given for the control. For each grid the difference (negative or positive) between its value and the control is given. Sample size in parentheses

Grids	'Onset'		'True'	
	Males	Females	Males	Females
Control (3)	82 (104)	92 (110)	74 (54)	86 (73)
Reduced cover (2)	-4 (83)	-5 (109)	+10 (50)	+4 (80)
Net - Cover (5)	+3 (124)	+1 (138)	-18 (63) ^b	-10 (96)
Net (4)	+2 (157)	-1 (142)	-15 (76)	+1 (112)
Net + Cover (6)	+6 (130)	+1 (131)	-11 (84)	-8 (113)
Net + Cover + Food (1)	+7 (147)	+4 (125)	-17 (98) ^b	-13 (131) ^a

Chi-square significant: ^a $P < 0.05$;
^b $P < 0.10$.

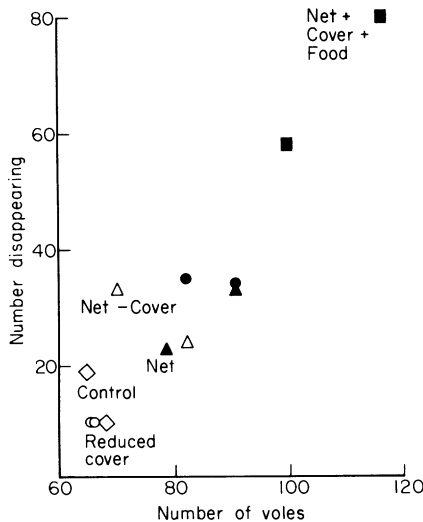


FIG. 4. The number of voles disappearing from grids during the period mid-March to mid-April ('true') and its relationship to population density on each grid: ■ = grid 1 (net + cover + food); ○ = grid 2 (reduced cover); ◇ = grid 3 (control); ▲ = grid 4 (net); △ = grid 5 (net - cover); ● = grid 6 (net + cover).

Wounding and movement

The amount of wounding in populations has been used as an indirect measure of intraspecific strife (Christian 1971). We have calculated the percentage of voles with wounds in each period of the spring decline (Table 6). In four out of six populations, more males were wounded in the 'true' breeding period than in the 'onset'. Wounding on the food grid was higher earlier because voles were breeding earlier on this grid. Few females ever had wounds in either period. This may not mean that there is no intra-female strife, but may indicate that subordination is achieved without repeated overt aggression which has been observed by Leuze (1976) in water voles (*Arvicola terrestris*, Lacepede).

TABLE 6. Percentage of voles with wounds in the 'onset' and 'true' breeding periods

Grids	'Onset'		'True'	
	Males	Females	Males	Females
Control (3)	30	4	28	1
Reduced cover (2)	34	10	44	12
Net - Cover (5)	26	4	56	11
Net (4)	26	9	40	9
Net + Cover (6)	39	16	52	13
Net + Cover + Food (1)	41	6	37	5

We calculated the mean movement of voles that were captured at least twice within a trapping period, then averaged these for the two periods (Table 7). Males on all grids moved further in the 'true' breeding period than in the 'onset'. On five out of six grids, females moved less in the 'true' breeding period than in the 'onset'.

TABLE 7. The average within trapping period movements of voles during the 'onset' and 'true' breeding periods. Distances in meters

Grids	'Onset'		'True'	
	Males	Females	Males	Females
Control (3)	5.0	4.4	5.9	3.3
Reduced cover (2)	3.8	2.8	6.7	2.1
Net - Cover (5)	2.5	3.2	3.2	3.4
Net (4)	2.7	2.3	4.5	1.7
Net + Cover (6)	3.4	3.2	4.2	2.8
Net + Cover + Food (1)	3.2	2.3	3.5	2.1

Weights

The weight distribution of males on the control and grid with extra food was the same before food was added (Fig. 5). But 2 weeks after food addition the average weight of males was significantly higher on the food grid (*t*-test, $P < 0.01$). The average weight of females was 46.0 g on the control and 46.7 g on grid 1 before food was added, but, like males, females were significantly heavier 2 weeks after food addition (*t*-test, $P < 0.01$) (two pregnant females on grid 1 were excluded from this analysis).

DISCUSSION

Populations of Townsend's vole on Westham Island in British Columbia are particularly interesting in that they exhibit both annual fluctuations and cycles (Krebs 1979). We looked for patterns in the spring decline that might allow us to predict which pattern of

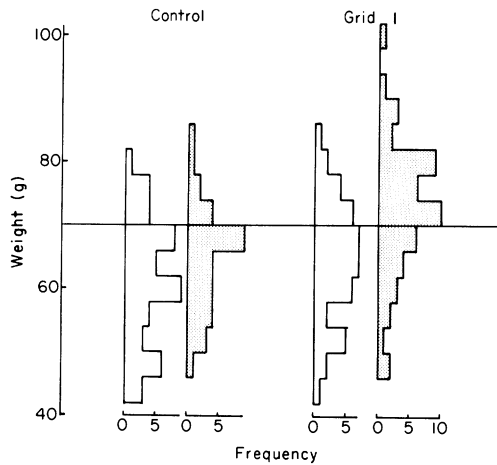


FIG. 5. Weight distribution of males on the control and the food grid before and after (shaded) food addition.

population dynamics would be exhibited in a given year (Taitt *et al.* 1981). Annual fluctuations in density appeared to be preceded by a substantial decline in both male and female density, while a cyclic pattern was preceded by some decline in male density but no decline in female numbers. Spring declines are thought to be the result of socially-induced mortality and dispersal (Krebs & Boonstra 1978), but what are the proximate mechanisms? We have conducted a series of experiments to explore the contribution of behaviour and extrinsic factors to spring population dynamics in this species.

Hormonal manipulations of behaviour did not produce major changes in the form of the spring decline. Although male voles were sensitive to reduced aggression in either sex; males had increased survival in a population where large males had been implanted with scopolamine Hbr (Gipps *et al.* 1981), and in a population where females had been fed a chemosterilant (Taitt & Krebs 1982). Females with testosterone implants had very high levels of wounding and low survival, but immigration was also high so that population numbers in the manipulated population were the same as in the control.

The results of the present study indicate that spring on Westham Island can be divided into two parts with the accompanying habitat features. The habitat features and demography of the vole population in these parts is summarized in Table 8.

TABLE 8. Summary of habitat features and vole demography in spring 1981

February to mid-March	Mid-March to mid-April
'Onset'	'True'
(i) av. rainfall over 100 mm/month, flooding	(i) rainfall less than 100 mm/month, no flooding
(ii) natural cover poor	(ii) natural cover improving
(iii) peak number of herons	(iii) few herons
'Onset'	'True'
(i) <30% of males breeding in first month	(i) >40% males breeding throughout
(ii) few if any females lactating	(ii) many lactating females
(iii) some wounding	(iii) peak wounding

Predation

The results of our extrinsic manipulations show that males in populations which are protected from predation have higher survival, higher immigration, and maintain higher densities than unprotected populations during the 'onset' (Fig. 3(a)). Further, when cover is reduced, survival is lower than in a control population (Table 5). Females in protected populations increase in number during this period and increase most where extra food is available (Fig. 3(b)). In the later 'true' breeding period, natural cover is improving and heron predation is probably unimportant.

Space and food

The addition of straw and straw plus food improved survival of voles in the 'onset' (Table 5). The highest number of voles was recorded on the grid with extra food. Reproduction was underway earlier on the food grid (Table 3) because voles were able to gain weight earlier than voles on other grids (Fig. 5).

Voles disappeared in a density-dependent manner across all experimental treatments in the 'true' breeding period (Fig. 4). At this time new habitat became available, male movements increased, male wounding peaked, female movement declined and many lactating females were present. Madison (1980), using radiotelemetry, found that reproductively active female *M. pennsylvanicus* had small exclusive territories. He suggested that such females might force males to forage in the interstices of their territories. If female *M. townsendii* behave in the same way, we suggest that reproductively active females may have caused the density-dependent dispersal observed in the 'true' breeding period. Male wounding may be intensified because males may be competing amongst themselves for oestrous females (Webster & Brooks 1981) as well as with the reproductively active females. This could also explain our previous behavioural results, namely good male survival in a population of docile males (Gipps *et al.* 1981) and in a population where females were made anoestrous (Taitt & Krebs 1982). Reproductively active females have high levels of blood steroids at this time (McDonald & Taitt 1982); this may enable them to dominate both males and immature females.

The density-dependent disappearance of voles in late spring (Fig. 4) provides the first field evidence of compensatory adjustment by spacing behaviour in vertebrate populations (condition d, Watson & Moss 1970).

Spring dynamics and cycles

The number of voles remaining in the population with extra cover plus food was 2.5 times the number on the control at the end of the spring decline. In the spring of 1975 which preceded the peak of a cycle of voles in this grassland, the density was 5 times the number in the previous 3 years which had preceded annual fluctuations (Krebs 1979). What would we have to do to limit the spring decline to the 1975 levels and thereby produce a cyclic high density breeding population?

First, the food that we provided was oats which is not the normal diet of herbivores. Although it was available at every trapping station its availability was restricted when compared with grass in a good grassland. In spite of these limitations, voles were able to gain weight such that 63% of males were over 70 g compared with only 23% on the control within 2 weeks of adding food (Fig. 5). Also, voles with oats became reproductive early and during the 'true' period produced 3.5 times as many potential immigrants as the control. Both of these phenomena are characteristic of cyclic vole populations increasing towards a peak (Krebs & Myers 1974).

Second, *M. townsendii* fulfil all the criteria of Watson & Moss (1970) (Taitt & Krebs 1981, present study), thus indicating that breeding populations are regulated by food and spacing behaviour. But an additional mechanism may be required to explain high breeding densities in cyclic years. We suggest that this could be simultaneous settling. Van den Assem (1967) showed that when many male sticklebacks were placed in a tank simultaneously, they established smaller territories than when they were added one by one over a period of time. Tompa (1971) suggested and Knapton & Krebs (1974) showed that simultaneous settling could take place in the territorial song sparrow (*Melospiza melodia*, Wilson). If voles are not aggressive until they become reproductive (Turner & Iverson 1973), and if food suddenly improves in an area so that large numbers of voles can become reproductive simultaneously, then settlement could be at a high pre-cyclic spring density. Further, if many young are produced by such voles, they may settle simultaneously at high density in any temporally suitable habitat. If simultaneous settling does contribute to generating some cyclic peaks, it might explain why high vole densities are not necessarily associated with increased levels of aggression (Hoffman, Getz & Klatt 1982).

Recruitment to the food population was biased towards females in contrast to all other grids where sex ratio was even. Females reached a peak of 3 times the control density (Fig. 3(b)). This indicates again that females are the first to respond to extra food (Fordham 1971; Taitt 1981; Taitt & Krebs 1981). We suggest that the number of mature females is closely related to the state of extrinsic factors, and if natural food and cover had been enhanced we might have observed simultaneous settlement and a female spring density similar to 1975 when the population in this grassland cycled.

It was suggested that winter flooding may impose temporal and spatial restrictions on space and food in this grassland (Taitt & Krebs 1981). Flooding forces voles into unflooded patches where they lose weight, stop breeding, and increase to a winter peak density. This study indicates that predation in early spring is high if cover is poor, but voles (especially females) with extra cover and food increase in density. Later in spring, when previously flooded patches dry out and grass starts growing, populations decline as some voles probably disperse into new habitat. Spacing behaviour, initially between males then between reproductive females and all voles, may 'decide' which are surplus. But, visibility to predators, food availability, and the extent of temporally suitable habitat may control the fate of the surplus (as prey, subordinates or dispersers), and hence whether the population fluctuates annually (substantial spring decline) or cycles multi-annually (small spring decline). While the habitat patchiness observed in *M. townsendii* may be unique, we suggest that simultaneous settling of the breeding population when extrinsic conditions are good, may be of general importance in cyclic species.

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REFERENCES

- Beacham, T. (1980). Dispersal during population fluctuations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, **49**, 867–877.
- Bujalska, G. (1973). The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility*, **19**(suppl.), 465–474.

- Christian, J. J. (1971). Fighting, maturity, and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **52**, 556–567.
- Fordham, R. A. (1971). Field populations of deer mice with supplemental food. *Ecology*, **52**, 138–146.
- Gipps, J. H. W., Taitt, M. J., Krebs, C. J. & Dundjerski, Z. (1981). Male aggression and the population dynamics of the vole, *Microtus townsendii*. *Canadian Journal of Zoology*, **59**, 147–158.
- Hoffman, J. E., Getz, L. L. & Klatt, B. J. (1982). Level of male aggressiveness in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus*. *Canadian Journal of Zoology*, **60**, 898–912.
- Knapton, R. W. & Krebs, J. R. (1974). Settlement patterns, territory size, and breeding density in the song sparrow (*Melospiza melodia*). *Canadian Journal of Zoology*, **52**, 1413–1420.
- Krebs, C. J. (1979). Dispersal, spacing behaviour, and genetics in relation to population fluctuation in the vole *Microtus townsendii*. *Fortschritte der Zoologie*, **25**, 61–77.
- Krebs, C. J. & Boonstra, R. (1978). Demography of the spring decline in populations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, **47**, 1007–1015.
- Krebs, C. J. & Myers, J. H. (1974). Population cycles in small mammals. *Advances in Ecological Research*, **8**, 267–399.
- LeDuc, J. & Krebs, C. J. (1975). Demographic consequences of artificial selection at the LAP locus in voles (*Microtus townsendii*). *Canadian Journal of Zoology*, **53**, 1825–1840.
- Leuze, C. C. K. (1976). *Social behaviour and dispersion of the water vole, Arvicola terrestris Lacepede*. Unpublished Ph.D. Thesis, Aberdeen University, Aberdeen, Scotland.
- Madison, D. M. (1980). Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioural Ecology and Sociobiology*, **7**, 65–71.
- McDonald, I. R. & Taitt, M. J. (1982). Steroid hormones in the blood plasma of Townsend's vole (*Microtus townsendii*). *Canadian Journal of Zoology*, **60**, 2264–2269.
- Sadleir, R. M. F. S. (1965). The relationship between agonistic behaviour and population changes in the deer mouse (*Peromyscus maniculatus*). *Journal of Animal Ecology*, **34**, 331–352.
- Saitoh, T. (1981). Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology*, **50**, 79–87.
- Taitt, M. J. (1981). The effect of extra food on small rodent populations: 1. Deermice (*Peromyscus maniculatus*). *Journal of Animal Ecology*, **50**, 111–124.
- Taitt, M. J., Gipps, J. H. W., Krebs, C. J. & Dundjerski, Z. (1981). The effect of extra food and cover on declining populations of *Microtus townsendii*. *Canadian Journal of Zoology*, **59**, 1593–1599.
- Taitt, M. J. & Krebs, C. J. (1981). The effect of extra food on small rodent populations: 2. Voles (*Microtus townsendii*). *Journal of Animal Ecology*, **50**, 125–137.
- Taitt, M. J. & Krebs, C. J. (1982). Manipulation of female behaviour in field populations of *Microtus townsendii*. *Journal of Animal Ecology*, **51**, 681–690.
- Tamarin, R. H. (1977). Dispersal in island and mainland voles. *Ecology*, **58**, 1044–1054.
- Tompa, F. (1971). Catastrophic mortality and its population consequences. *Auk*, **88**, 753–759.
- Turner, B. N. & Iversen, S. L. (1973). The annual cycle of aggression in male *Microtus pennsylvanicus* and its relation to population parameters. *Ecology*, **54**, 967–981.
- Van den Assem, J. (1967). Territory in the three-spined stickleback *Gasterosteus aculeatus*. *Behaviour Supplement*, **16**, 1–164.
- Watson, A. & Moss, R. (1970). Dominance, spacing behaviour, and aggression in relation to population limitation in vertebrates. *Animal Populations in Relation to their Food Resources* (Ed by A. Watson), pp. 167–218. Blackwell Scientific Publications, Oxford.
- Webster, B. A. & Brooks, R. J. (1981). Social behaviour of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62**, 738–751.

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APPENDIX 1

Total monthly precipitation (mm) for Vancouver Airport (10 km north of study area).

Month	30-year average	1980/81
October	122	58
November	141	311
December	165	232
January	147	72
February	117	156
March	94	126
April	61	143
May	48	82