Predation on *Microtus townsendii* populations: impact and vulnerability

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The object of this study was to assess the impact of avian and mammalian predators on *M. townsendii* populations, especially during decline periods. In addition, Errington's hypothesis of differential susceptibility of certain classes of animals to predation was examined. The vole population went through a severe decline in the winter and spring of 1972–1973 and again in the winter and spring of 1973–1974. Intensive searches were made for all pellets and scats from February 1973 to May 1974.

Of the tagged animals disappearing, less than 8% in the decline of 1972–1973 and less than 20% in the decline of 1973–1974 could be accounted for by predation. I conclude that predation is not necessary to initiate or maintain a decline. In the tagged animals, neither sex nor any weight class showed any consistent vulnerability to predation when compared with the rest of the tagged population. In the total sample of voles eaten by avian predators, the body weights were consistently lower than those in the trapped population. In the other life-history characteristics examined, voles were eaten at random. I conclude that no animal was more vulnerable to predation than another in the tagged population, but in the total population younger animals may have been.

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On a tenté de mesurer l'impact des prédateurs, oiseaux ou mammifères, sur les populations de *M. townsendii*, surtout dans les périodes de déclin. On a examiné également l'hypothèse d'Errington concernant la susceptibilité différentielle de certaines classes d'animaux à la prédation. La population de campagnols a subi une forte baisse durant l'hiver et le printemps de 1972–1973 et ceux de 1973–1974. On a procédé à une recherche très active de toutes les fèces et régurgitations de février 1973 à mai 1974.

Parmi les animaux marqués disparus, moins de 8% durant le déclin de 1972–1973 et moins de 20% durant le déclin de 1973–1974 ont été tués par des prédateurs. On en conclut que la prédation n'est pas un facteur indispensable au déclenchement ou au maintien du déclin d'une population. La vulnérabilité à la prédation ne peut être reliée ni au sexe, ni à la classe d'âge, chez les animaux marqués disparus, comparativement au reste de la population marquée. Si l'on considère l'ensemble de l'échantillon de campagnols mangés par les oiseaux, les poids sont toujours plus bas que chez les campagnols de la population capturée. La prédation se fait au hasard en ce qui concerne les autres paramètres vitaux. On croit que tous les animaux de la population marquée sont également vulnérables à la prédation, mais que, au sein de la population totale, les animaux les plus jeunes sont peut-être plus vulnérables.

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Introduction

The impact of predators on prey continues to be a subject of theoretical and experimental interest (see Huffaker (1971) and Murdoch and Oaten (1975) for reviews). In the study of microtine cycles, there are diverse opinions on the importance of predation, ranging from the belief that predation truncates population peaks and causes decline periods (MacLean *et al.* 1974),

to the belief that predation acts only after some other agent has started the decline and then serves to depress the population in low periods (Pearson 1966, 1971), to the belief that predation is not necessary for the decline (Chitty 1960). The first objective of this study was to assess the impact of both mammalian and avian predators on *Microtus townsendii* populations, especially during population declines. Most other studies on this topic have dealt only with either mammalian predators or avian predators but not both, so that the total effect of predation on a particular population was not known.

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A second objective was to determine if predation was selective on certain members of the vole population. Errington (1956) believed that some segments of an animal population were more vulnerable because of their position in the social hierarchy. These individuals were doomed to death by one agent or another, with predation being only one of the causes. In contrast with this, Pearson (1966) believed that carnivores preying on *Microtus* populations are capable of catching not only sick, homeless, or socially subordinate animals, but also healthy resident animals. No study has intensively followed a marked population of voles to obtain life histories of the animals, and then related this to subsequent predation. In this study, marked vole populations were trapped every 2 weeks, and during the fall and winter, all evidence of predation (pellets and scats) was collected.

Methods

The study area was on Westham Island in the Fraser River delta, near Vancouver, British Columbia, on a 37-acre (15-ha) parcel of grassland owned by the Department of National Defence as a transmitter-receiver site. The area is relatively flat, has a number of drainage ditches running through it, and is enclosed by fences. It is surrounded by cultivated fields to the east and south, a salt marsh and the sea to the west, and a waterfowl sanctuary to the north. The only nearby areas where voles can live are a permanent pasture (about 6 ha in size 170 m to the south) which, because of intensive grazing by cattle in the summer, probably contained few voles, and small grass margins occasionally occurring along the dykes. The vole population on the study area is thus relatively isolated (see LeDuc and Krebs (1975) for an aerial photograph of the area). Livetrapping of this *M. townsendii* population has been carried out since July 1971.

The general technique involved livetrapping voles on 1.7-acre (0.7-ha) grids. Each of 100 trapping points was located 25 ft (7.6 m) from the next. Additional traps (up to 100 per grid) were added as vole density increased. Longworth live traps were baited with oats; cotton stuffing was provided for warmth. The traps were set every 2nd week in the afternoon, checked the next morning, the next afternoon, and again on the second morning, when they were locked open and left in place. During the summer, traps were set only in the evenings to avoid mortality in traps during the heat of the day. All voles were ear-tagged (aluminum tags), and the trap location, sex, reproductive condition, and weight of each animal were recorded. In this paper, unless otherwise indicated, animals are classified as adult (> 42 g), sub-adult (30 g to 42 g), or juvenile (< 30 g). Population statistics were determined by enumeration techniques to avoid statistical assumptions of random sampling. These statistics are believed to be accurate because of high trappabilities (> 80%) in winter, when most of the detectable predation occurred (Hilborn *et al.* 1976).

Bird pellets and carnivore scats were collected on the study area from February 1973 to May 1974. The area was searched thoroughly about once per month by walking along all fence lines, paths, ditches, roadways, underneath antenna guy lines, and arbitrarily over the fields, as well as through trapping grids. On the study area there were only a few clumps of shrubs and trees which could have served as roosts. However, trees did occur on the dykes and in the waterfowl sanctuary. Information was obtained from the sanctuary's naturalists who collected pellets every 2-3 months from roosts in these trees and from roosts in local farm buildings. I searched fence lines, ditch margins, and dykes on the pasture south of the main study area every 2-3 months, as well as neighboring farm fence lines. I am reasonably confident that most of the pellets and scats deposited during the winter were found because heavy rains flattened the standing grass, making them easy to see. I found no evidence that scats were buried. A few pellets and scats were probably missed each time I collected and may have been collected in a subsequent search. Therefore the data are grouped into broad periods of time. With the growth of grass in April, my ability to find pellets and scats decreased markedly so that the data from late spring and summer give no true indication of the actual extent of predation. I did not expect any pellets or scats to survive from one winter to the next because of high rates of decay in summer. However I assumed that pellets and scats deposited in late fall and winter would remain relatively intact until spring. Of the pellets collected in February 1973, very few showed signs of weathering.

Therefore, the majority of the predation which I was able to detect occurred during the fall, winter, and early spring. Every fall there is an influx of raptors from northern Canada and Alaska, some of which presumably spend the winter in this area. The major avian predators seen on the area were short-eared owls (*Asio flammeus*), great-horned owls (*Bubo virginianus*), snowy owls (*Nyctea scandiaca*), barn owls (*Tyto alba*), marsh hawks (*Circus cyaneus*), rough-legged hawks (*Buteo lagopus*), red-tailed hawks (*Buteo jamaicensis*), northern shrikes (*Lanius excubitor*), and great blue herons (*Ardea herodias*). I made no attempt to distinguish between the pellets of any of these species, since there was considerable size overlap between some of them. Feral cats (*Felis catus*) and raccoons (*Procyon lotor*) were the only two carnivores known to occur on the area. Contents from their scats were also pooled. No weasels were ever caught on the trapping area.

Each avian pellet was analyzed separately. The first 300 pellets were soaked in water and picked apart. All other pellets and all scats were soaked for 24 h in 10% potassium hydroxide. The slurry was then poured over a fine screen mesh, and washed with a gentle stream of water to remove digested hair and feathers. All skulls, mandibles, innominate bones, ear tags, and incisors were saved.

Results

Incidence of Predators

Feral cats were occasionally seen on the study area in both winters. The warden from the waterfowl sanctuary destroyed all cats and

TABLE 1. Total number of prey collected from pellets and scats on the study area. The number of voles eaten by avian predators was calculated by counting only the number of paired mandibles found. The number of voles eaten by mammalian predators was calculated by counting pairs of upper incisors

	Feb.-April 1973	May-Sept. 1973	Oct.-Dec. 1973	Jan.-May 1974	Total
Pellet contents					
<i>Microtus townsendii</i>	491	40	320	338	1189
Bird (unidentified)	17	2	31	11	61
Shrews	25	3	15	15	58
Rats	5	3	3		11
Deer mice	5		2		7
Insects (unidentified)	8				8
Other			2	1	3
Scat contents					
<i>Microtus townsendii</i>	33	4	31	167	235

raccoons seen or caught on the sanctuary or adjacent areas. In January 1973 a feral cat was living underneath buildings adjacent to control grid I. This animal was trapped and removed on January 24 because it disturbed traps used in the livetrapping program. No cats were observed until January and February 1974, although scats from these animals were found in December. In January another cat began living underneath the same buildings. It temporarily left the area at the end of February, returned in mid-March, and was destroyed by the warden in May. In both springs, raccoons were common around the sanctuary, raiding eggs from nesting waterfowl, and occasionally wandering out onto the study area, and opening set traps. However, in both springs the incidence of this was low.

I recorded birds of prey sighted on the study area while I was trapping, and got additional information from the sanctuary. The most common diurnal birds of prey during the fall and winter of 1972-1973 and 1973-1974 were short-eared owls and marsh hawks. One or two short-eared owls were sighted every time the study area was visited. Lockie (1955) and Clark (1975) have suggested that this species forms winter feeding territories, and thus birds seen on my study area may have been permanent winter residents. One or two marsh hawks were also seen during each visit to the area and these were thought to be resident throughout the year, nesting in the nearby salt marsh. Craighead and Craighead (1956) and Schipper *et al.* (1975) report that in winter, this species also has restricted hunting areas. Red-tailed and rough-legged hawks were

occasional visitors. Barn owls and great-horned owls were never seen on the area, but were known to be roosting in local farm buildings and in the woods on the sanctuary. One and occasionally two herons were seen hunting on the area in winter. These birds were also known to roost in conifers in the sanctuary, where some of their pellets were collected. Altogether there were between three and five avian predators regularly on the area.

Amount of Predation

The prey items found in pellets and scats on the study area are shown in Table 1. Pellets collected from nearby areas had similar contents: 222 voles, 30 birds, 8 shrews (*Sorex vagrans*), 5 rats (*Rattus norvegicus*), 2 deer mice (*Peromyscus maniculatus*), 1 insect, and 1 unidentified prey item. Between 300 and 400 pellets were also analyzed by naturalists from the sanctuary and similar contents were found. *Microtus townsendii* accounted for the greatest number of prey recovered during this study. The table indicates that there were few alternative prey species besides the vole. Waterfowl were plentiful in adjacent areas, but were not heavily preyed upon. Shrews were common but at very low densities (two to six per hectare). Rats were uncommon but were occasionally trapped along ditch margins. Deer mice were trapped only along dykes with trees and were believed to be at low densities.

Pellet contents from certain birds of prey may contain fewer prey items than are actually eaten. Pellets of hawks generally contain less bony

TABLE 2. Number of voles disappearing from study area and percentage recovered from predators

Period	Grid	No. disappearing	% recovered from all predators	% recovered from:		
				avian predators	mammalian predators	total
Dec. 1972 - April 1973	H	129	3.1			
	G	204	5.9			
	I	230	7.4			
Oct. - Dec. 10, 1973	I	132		12.9	17.4	30.3
Dec. 22, 1973 - April 1974	I	253		3.2	15.8	19.0

To see if tags were lost in the feeding process, I fed dead voles to two tame short-eared owls. Out of 29 tagged voles fed to the owls, 24 tags were recovered in pellets. The owls decapitated some of these voles and dropped their heads from perches; in at least one case the head was not eaten later. Since I never found severed heads in the field, the tag loss in the experiment may be an artifact. Some bird species, such as marsh hawks, are known to pull hair from the prey before ingesting the carcass (Clark 1972). I thoroughly searched every kill of this nature and never found ear cartilage or tags. During the entire study, partly consumed voles were very infrequently found. Tag losses from voles caught by predators were probably few, and I estimate less than 20%.

During the decline of 1973 only about 1% of the tagged animals which disappeared was subsequently recovered in mammalian scats. The data from avian and mammalian predators were therefore pooled. During the decline of 1974, a much larger proportion of the disappearance was due to mammalian predators, so that a distinction was made between voles eaten by the two classes of predators. Table 2 shows that less than 8% of the voles disappearing from the trapped populations during the 1973 decline could be attributed to predation. In 1974, on grid I, more than twice as much of the disappearance could be attributed to loss by predation, largely because of the cat living adjacent to the grid. However in both declines, the population on grid I peaked and declined to almost identical levels. The average rate of decline per week was 8% in 1973 and 11% in 1974. This suggests that the more intensive predation during the second decline did accentuate the rate of loss.

To examine more closely how predation affected survival of the voles on control grid I

in the fall and winter of 1973-1974, I compared the changes in survival rate with loss due to predation. Poor survival is arbitrarily defined to be any rate below 0.707 per 2 weeks (half of the population disappearing every 4 weeks). Data for both sexes were combined because minimum survival rates were similar for most of that period. The correlation between the minimum survival rates and the percentage of loss owing to predation over the winter was poor ($r = -0.21$, $n = 15$). From October 1973 to the end of January 1974, survival was good, averaging 0.81 per 14 days (Fig. 2). This compared with a minimum survival rate of 0.85 in 1972-1973 when predation was less intense. During February, minimum survival rates remained high at 0.80 per 14 days, while loss of animals due to predation was negligible (0.02). In the next 1.5 months, the minimum survival rate dropped drastically so that the mean for this time was 0.65 per 14 days, while the total loss due to predation was small (0.10). In two of the three trapping intervals no loss to predation was observed at all. This coincided with the absence of a cat. Thus predation is not necessary for population declines to occur, since periods of poor survival occur in the absence of detectable predation, and periods of good survival occur in the presence of predation.

To see if the amount of predation by birds was similar in the tagged and untagged population on the study area, I made the following calculations. Because there was some variability in vole densities on various parts of the study area owing to excessive local flooding in winter, I took the average of the number of voles disappearing between October 1972 and April 1973 from grids G, H, and I as an index of the number disappearing from the entire area. In 1973-1974, the number of voles disappearing from the entire

FIG. 2. (A) Minimum survival rate per 14 days for both sexes combined during fall and winter, 1973-1974. The horizontal line is drawn at a rate of 0.707, below which half the population disappears every 4 weeks. (B) The number of voles disappearing every 14 days during fall and winter, 1973-1974. The blackened portions indicate the number of animals known to have been eaten by predators.

study area was estimated from the number disappearing from control grid I and I corrected this downward by a factor (0.88) equivalent to the amount that grid I had been reduced in 1972-1973 to make it equal to the average for that time. Table 3 shows that, in both winters, raptors ate at least about 11% of the voles estimated to have been lost from the whole area. The table also shows that they ate only 6% of the voles lost from the tagged population (difference between total and tagged predation in 1972-1973, $\chi^2 = 12.55$, $P < 0.001$; difference in 1973-1974, $\chi^2 = 6.05$, $P < 0.05$).

This difference in losses between the total and the tagged populations may be explained by the following. (1) The percentage recovery of the tagged voles may be too low. This could occur if one assumes that for each vole caught on the area and deposited elsewhere, another vole is caught elsewhere and deposited on the area, and that this type of interchange between areas is high. A great number of tagged voles would therefore be deposited elsewhere. For reasons already stated, I believe that this error was small. (2) The percentage recovery of all voles may be too high. This could occur if a segment of the population, such as the young, is not trappable but is subject to predation. Evidence supporting this explanation is presented below. (3) The tags may have been lost. For reasons

TABLE 3. Comparison of avian predation on the entire vole population with that on the tagged portion of the population

	Winter 1972-1973	Winter 1973-1974
No. of voles disappearing per hectare	348*	491†
No. of hectares	12.96†	12.15§
Total no. of voles disappearing	4510	5966
No. of voles found in pellets	491	658
% of total number of voles disappearing which were recovered in pellets	10.9	11.0
% of tagged voles disappearing which were recovered in pellets	6.1	6.5

*Obtained from the average of three trapping grids, G, H, I.
†Area occupied by road, buildings, ditches, and low-density experimental grids excluded.

‡Obtained from the number of voles disappearing from grid I, corrected for heterogeneity of habitats.

§In addition to the areas described above, † one new low-density experimental grid excluded.

stated previously, I also believe that this loss is low.

Selectivity of Predation

To determine if certain classes of voles were more vulnerable to predation than others, I removed over 900 animals from the population during the study for autopsy purposes. After autopsy, the skull and innominate bones of each

TABLE 4. Sex ratio comparison of voles on the control with that of voles eaten by predators. Data presented as the number of males per female. The total avian sample includes all voles which could be sexed. The pooled tagged samples include the tagged samples eaten by both avian and mammalian predators. Sample sizes are in parentheses

Period	Control grid	Total avian sample	Pooled tagged sample	Tagged mammalian sample	Tagged avian sample
Winter 1972-1973	0.58 (2063)	0.77* (362)	1.29** (48)	2.0 (9)	1.17* (39)
Fall 1973	0.91 (1233)	0.88 (357)	1.65 (45)	1.14 (15)	2.00 (30)
Winter 1974	0.90 (895)	0.89 (104)	0.74 (66)	0.78 (58)	0.60 (8)

* $P < 0.05$ for hypothesis of equal sex ratio to that found on control grid.

** $P < 0.01$.

vole were cleaned by dermestid beetles. I recorded seven measurements for each vole whenever possible: mandibular height, mandibular length (both according to the method of Lidicker and MacLean 1969), innominate length, rostrum length from the outer edge of the incisors to the end of the mandibular tooth row, ischium length from the posterior angle of the ischium to the nearest edge of the acetabulum, pubis length from the ventral apex of the pubis to the nearest edge of the acetabulum, and pubis width at the thinnest part (the latter three measurements are described in Dunmire (1955)). These measurements were chosen because they could also be taken from most of the voles consumed by birds. No measurements were made from voles eaten by carnivores as few whole bones were found. Mandibular height, rostrum length, and innominate length were eliminated after preliminary analysis indicated that they were not useful for predicting either sex or body weight.

Sex Ratio

To predict sex of unknown animals, I used a stepwise discriminant analysis program (program BMD 07M, Health Sciences Computing Facility, University of California at Los Angeles). Measurement (in millimetres) of pubis length and pubis width were sufficient to predict sex in the known sample 96.55% of the time. The classification function is as follows:

$$X = 19.38 (\text{pubis width}) - 1.751 (\text{pubis length}) + 1.390$$

with animals having $X > 0$ being male and $X < 0$ being female. Of the more than 900 autop-

sied voles, a higher percentage of males (5.9%) than females (1.1%) was misclassified. In males, a higher proportion of the small animals was misclassified than of the large animals ($\chi^2 = 21.21$, $df = 3$, $P < 0.001$), indicating that differences between males and females were more distinct in larger animals. Misclassification of females was not more pronounced in small animals ($\chi^2 = 4.49$, $df = 3$, $0.10 > P > 0.25$). To correct for the misclassification of animals, I added 4% of the animals classified as females to those classified as males.

The data for this section are broken down into three periods to coincide with major changes in population trends and to coincide with the way the pellet and scat data were collected. The data used from the control grid cover the following periods: (1) winter 1973 (October 15, 1972-April 30, 1973); (2) fall 1973 (September 17-December 24, 1973); and (3) winter 1974 (January 7-April 15, 1974).

To see if predators selectively removed one sex from the population, I compared the sex ratio of resident animals on grid I with (1) the sex ratio of all voles recovered from the pellets of avian predators; and (2) the sex ratio of tagged animals eaten by avian and carnivore predators. The sex ratio of the resident control population was the minimum number of animals of each sex known to be alive at every trapping period, pooled over the entire period. Table 4 shows that there is no consistent trend in the selectivity of either class of predators for one sex. In winter 1972-1973, males were selectively eaten by both mammalian and avian predators in both the tagged sample and in the untagged samples.

In winter 1974, the sex ratio of both the tagged samples eaten by the two classes of predators and the total sample eaten by avian predators was not significantly different from the sex ratio on the control. The difference between the years may be the result of small sample sizes, or the pooling of the data for 1972–1973, thus obscuring any difference between fall and winter. However, the populations in the 2 years appear to be quite different with regard to sex ratio.

Body Weight Distributions

To see if certain size classes of voles were more vulnerable to predation by avian predators than others, I used multiple regression analysis to develop equations to predict the body weight of voles I was able to sex. The sample of over 900 standards was divided into the two sexes and into four blocks of data corresponding to two periods each of breeding and nonbreeding in which the individuals were collected. Because the innominate bone was used to predict sex, and because I could not assume that a skull and a set of innominate bones in a pellet necessarily belonged to the same vole, weight of the sexed animals was predicted only from measurements made on the innominate bones. A cube root transformation was done on body weight in the standards to linearize the equations. In males there was no significant difference between the four blocks of data when the three measurements explaining the greatest amount of variability were used ($F = 0.09$, $df = 12, 437$). The equation for the pooled data was

$$\sqrt[3]{\text{body weight of males}} = 1.023 + 0.1926 (\text{pubis width}) + 0.1584 (\text{pubis length}) + 0.1523 (\text{ischium length}).$$

The equation had a coefficient of multiple determination of 0.73. In the female standards, there were significant differences between regressions for reproductive and nonreproductive periods. Because most of the predation I was able to detect occurred in the nonbreeding period, I used only the female standards collected during that time to develop multiple regression equations. As there were significant differences between the female standards in the two nonbreeding periods, a separate multiple regression was developed for the 1972–1973 data and for

TABLE 5. Mean body weight ($g \pm SE$) of voles on the control grid and those eaten by predators. Total avian sample includes all voles which could be sexed. Sample sizes in parentheses. Pooled tagged sample includes all tagged voles eaten by both avian and mammalian predators. Weights of animals eaten by avian predators were predicted by measurements made on innominate bones

Period	Control grid	Total avian sample	Pooled tagged sample
Males			
Winter 1972–1973	46.4 ± 0.4 (687)	$43.6 \pm 1.0^*$ (148)	46.2 ± 1.8 (27)
Fall 1973	51.2 ± 0.5 (542)	$37.5 \pm 0.8^{**}$ (159)	$45.5 \pm 2.4^*$ (21)
Winter 1974	52.4 ± 0.6 (381)	$40.4 \pm 1.4^{**}$ (47)	$45.2 \pm 2.2^*$ (29)
Females			
Winter 1972–1973	40.2 ± 0.2 (1146)	$35.8 \pm 0.4^{**}$ (216)	39.6 ± 2.0 (21)
Fall 1973	46.5 ± 0.4 (585)	$35.8 \pm 0.6^{**}$ (199)	46.5 ± 3.1 (13)
Winter 1974	41.0 ± 0.4 (423)	$35.8 \pm 0.9^{**}$ (60)	39.7 ± 1.4 (34)

* $P < 0.05$ for hypothesis that control mean weight is equal to mean weight of sample eaten by predators.

** $P < 0.001$.

the 1973–1974 data. The 1972–1973 multiple regression was

$$\sqrt[3]{\text{Body weight of females}} = 1.7262 + 0.1366 (\text{pubis length}) + 0.0662 (\text{ischium length})$$

with a coefficient of multiple determination of 0.57. The equation for the 1973–1974 data was

$$\sqrt[3]{\text{body weight of females}} = 1.5148 + 0.1427 (\text{pubis length}) + 0.0973 (\text{ischium length})$$

with a coefficient of multiple determination of 0.72. In both cases, pubis width was not significant and was eliminated from the regressions.

The mean body weight of animals from the control grid was obtained by summing the body weights of every animal caught during a given period and dividing by the total number of animals. This was therefore a mean cumulative body weight. Table 5 shows that the total sample of both male and female voles eaten by avian predators was significantly lower in all periods by 2.8–13.7 g than the mean body weight in the

same period on the control grid (Mann-Whitney U test). There was no significant difference in mean body weights between the tagged sample eaten by carnivores and the tagged sample eaten by avian predators so only the pooled data are given in Table 5. The pooled tagged sample had mean body weights that were consistently higher than the mean body weights of the total sample eaten by avian predators. This difference was significant in fall 1973 in males, and in females in fall 1973 and winter 1974. The mean body weight of the pooled tagged sample was similar to the mean body weight of the control, except for fall 1973 and winter 1974 in males, when they were lower. With these two exceptions, this suggests that with regard to body weight, the tagged animals in the control population were being caught at random by predators. It also suggests that avian predators were either selectively catching the smaller segment of the population which was not tagged, or our trapping was selectively catching the larger animals.

The large proportion of small animals in the sample eaten by predators becomes even more obvious when the data are analyzed with a simple regression to predict body weight based on mandibular length. The above multiple regression equations were useful only in cases in which innominate bones were present so that sex could be determined. In young voles, the innominate bones are very fragile, and few of them survive the digestion process of avian predators. Mandibles, on the other hand, are not digested so much, with most remaining relatively intact. To get a rough indication of the size distribution of the total sample eaten by avian predators, I developed a simple regression using standards from the two nonbreeding periods and lumping both sexes. A cube root transformation was done on body weight to linearize the regression. The equation was

$$\sqrt[3]{\text{body weight}} = -2.0477 + 0.2986$$

(mandibular length)

with a coefficient of determination of 0.65.

Of the 1343 individuals found in pellets on all areas, only 989 could be sexed. Of the remainder, 237 (17.6%) had a predicted body weight of ≤ 20 g. Figure 3 shows that the body weight distribution of voles eaten during the fall and early winter of 1973 was decidedly in favor of

FIG. 3. Body weight distributions of animals (both sexes combined) trapped on the control grid and captured by avian predators, fall and early winter 1973-1974. Weights of voles eaten by predators were predicted from mandibular length.

small animals, whereas on the control grid the cumulative body weights for both sexes for the same period favored large animals. The cumulative body weights on the control are the summation of the body weights of each animal every time it was caught. The data from other periods showed similar differences between the two groups.

Predation on Tagged Voles

To see if the tagged voles eaten by predators differed in some way from tagged voles not known to have been eaten, I compared these two groups with respect to the information collected about the voles. Specifically, I examined for differences between these two groups with regard to: (1) movements between trapping periods; (2) movements within trapping periods; (3) mean body weight at first capture; and (4) average duration of life. Unfortunately, the small sample sizes and the high variability within any given

class obscured any consistent differences between the two groups for all variables considered. Because of this the data will not be presented here. I conclude that, with regard to the above variables and the inherent constraints in the trapping technique, both avian and mammalian predators were selecting the voles at random from this population.

Discussion

This study provides no support for the hypothesis that predation is necessary to start a decline or to keep it going. The vole population in the 2nd year, when predation was more intense, had higher rates of loss than in the 1st year. Predation may thus have accentuated the decline in the 2nd year. However, during the second decline, periods of poor survival occurred in the absence of predation, and periods of good survival occurred in the presence of predation. This suggests that some other agent was responsible for the declines.

The predators associated with the two declines were very different. In 1972–1973 the major predators were primarily birds of prey, whereas in 1973–1974 they were primarily mammalian carnivores. The intensity of mammalian predation during certain weeks suggests that these predators could potentially depress the population.

Many workers have emphasized the importance of mammalian predators, which, because they lack the mobility of avian predators, are forced to stay on an area while a vole population is declining. In winter, in areas where snow cover is continuous and lasts a long time, continual pressure by weasels is postulated to be the major influence in depressing microtine densities in decline periods (Thompson 1955b; Maher 1967; Fitzgerald 1977; MacLean *et al.* 1974). In none of these studies, however, were the microtine populations actually studied during the winter. Rather, the importance of weasels was inferred from the presence of disturbed microtine winter nests. To test the hypothesis that weasel predation is necessary for declines in the north, one could enclose a microtine population with a predator-proof fence just before an expected decline. The fate of individuals during a decline might also be obtained by radioactively tagging a microtine population, thereby more accurately determining the amount eaten by weasels

(Hilborn and Krebs 1976). However in the latter suggestion, scavenging foxes might confound the results by eating animals that died from other causes.

In areas where there is little or no snow, larger carnivores are thought to be the important agents of mortality. An intensive study on predation in microtines (Pearson 1964, 1966, 1971) emphasized the importance of the less mobile mammalian predators. Pearson contends that during the increase and peak periods of a typical cycle, predation tends to be independent of density. During the decline, predation intensifies as densities drop, and maintains the vole population at low densities for some time thereafter. Essential to the continued predation pressure at low densities is the presence of alternative prey to sustain these predators while they continue to hunt for the remaining voles. Thus, Pearson believes that predators help determine the periodicity of the cycle by determining its amplitude and the duration of the phase of low numbers. My Westham Island population of *M. townsendii* does not appear to respond as Pearson's ideas predict. Carnivore predation on my study areas was sporadic because of predator removal on the adjoining sanctuary. No weasels existed on the study area. Severe population declines occurred nonetheless, and the declines I observed were more severe than the declines observed in nearby populations of *M. townsendii* which have weasel predation (Krebs *et al.* 1976). The absence of continuous carnivore predation and of alternative prey species on Westham Island may be one of the reasons for the immediate increase in numbers at the end of each decline period in this study. None of the *M. townsendii* populations studied in the delta region have had extended periods of low numbers (LeDuc and Krebs 1975; Krebs *et al.* 1976).

What happens to all the animals that disappear in a decline, if predation is insufficient, as in the present study? Very little dispersal to nearby vacant areas occurred in declines observed by Chitty and Phipps (1966), Myers and Krebs (1971), and Hilborn and Krebs (1976). Therefore, voles are either dying *in situ* from unknown causes or they are dispersing long distances. Hilborn and Krebs (1976) suggest that the latter explanation may indeed be responsible for one of the decline periods they observed. Fencing in a population that is predicted to decline would

allow one to distinguish between these two alternatives.

Predators are able to affect the prey population directly by removing large numbers, and indirectly by altering the age and sex structure of the population, thus changing the dynamics of the population. Sometimes one sex survives less well than the other, with males frequently declining before females (Chitty and Phipps 1966; Krebs 1966; Krebs *et al.* 1969). This was also the case in this study. For example, during the first 2 weeks of April 1974, males had a minimum survival rate of 0.40 per 14 days ($n = 20$) while females had a minimum survival rate of 0.80 ($n = 25$). This poor survival in males was associated with an earlier onset of breeding condition. Several workers have found selection by various predators for a specific sex which may explain some of this differential survival. Thompson (1955a) found selection by snowy owls for male brown lemmings (*Lemmus sibiricus*) during the early summer, but not during the late summer. He suggested that this difference was due to the greater movement and thus exposure of the males in early summer. MacLean *et al.* (1974) found some evidence of heavy predation by weasels on breeding brown lemming females, which, if it were widespread, could depress the rate of increase of the population. Stendell (personal communication), in a study of raptor predation in California, found that in short-eared owls there was no preference for either sex compared with the trapped population, whereas in barn owls there was a preference for males. In none of the other studies on microtines have workers found selective predation on either sex (Southern and Lowe 1968; Maher 1970). In the present study, there was no consistent selection by either mammalian or avian predators for either sex between periods, although it may be that selection for a given sex was indeed occurring by different bird species, but in different directions for different species, so that lumping the data obscured the selection.

A number of workers have also looked at selection by predators for various age classes. Lockie (1955) found that in the spring, short-eared owls took small animals in the same proportion as the traps did. However, in the summer, the owls were taking a much higher proportion of young than that occurring in the traps. In the other studies, no evidence of size selection was

observed (Southern and Lowe 1968; Saint Girons 1973; Stendell, personal communication). In the present study, in the total sample of voles eaten by avian predators there was a consistent selection for smaller animals (Table 5, Fig. 3). Because predation on the tagged population appeared to be random with regard to body weight, these results suggest that either the trapping scheme was selecting larger animals or that avian predators were selecting smaller animals. To distinguish between these two alternatives, a technique for catching small animals in fall and winter would be necessary. Data presented in Boonstra (1976) indicate that Longworth live traps during the summer catch mainly larger animals whereas pitfall traps catch large numbers of younger animals. This suggests that a trap bias toward larger animals is present. However, in addition to this, birds of prey may be selecting young animals heavily. If this is so, especially during the fall increase period, this might cause a subsequent decline, for there would be few young to replace the older animals disappearing gradually over the winter from normal causes of mortality. Selective removal of the young would reduce the number of pre-reproductives and thus have a disproportionate effect on the future density of the population. However, because the total predation on the study area was estimated to have been low (Tables 2, 3), this selection, if it were occurring, would probably be of minor importance in determining population processes.

Errington (1956) proposed that predators do not remove individuals from prey populations at random, but rather remove those individuals that are vulnerable because of their position in the social structure of the population. Jenkins *et al.* (1964) found support for this argument in red grouse, where nonterritorial, dispersing birds were selectively removed by avian and mammalian predators, while territorial birds were relatively safe. Periods of dispersal in small mammals are thought to be times when predation is particularly important (Blair 1953; Errington 1967). Metzgar (1967), working on *Peromyscus leucopus*, and Ambrose (1972), working on *M. pennsylvanicus*, have found that animals unfamiliar with the habitat were removed more often by the avian predators. In my study, of the 40 tagged animals known to have dispersed from one grid to another, only two did

so during either of the decline periods. This suggests that most of the animals disappearing during the declines were dying *in situ*, and that the animals disappearing because of predation were killed on the grid and so were presumably familiar with the habitat. It may be, however, that the reason little dispersal was observed during the declines was because of intense predation on dispersers, so that the majority never reached another grid.

Selective predation on members of the vole population may be related to positions of dominance, predisposing subordinate individuals to various forms of mortality. In an experimental study on the effect of social position on susceptibility to predation in cotton rats (*Sigmodon hispidus*), Roberts and Wolfe (1974) found that a feral cat selectively killed dominant individuals, whereas a red-tailed hawk selectively killed subordinate animals. In *M. pennsylvanicus*, Turner and Iverson (1973) found that the heavier animals were generally dominant. In my study, in the tagged segment that was eaten by predators, there was no selection for lighter females, whereas there was selection for lighter males in the fall and winter of 1973–1974. There were no differences in the demographic characteristics examined between the tagged segment eaten by predators and that not known to have been eaten. Therefore this study provides no support for Errington's hypothesis of nonrandom predation. However, the social position of individuals eaten by predators is unknown. A more rigorous test of Errington's ideas would be to obtain behavioral profiles of individuals in large enclosures in a manner similar to that of Krebs (1970) and Turner and Iverson (1973) and subject these animals to predation.

Predation by raptors on voles may be viewed as essentially a random process, at least with regard to the tagged population. A vole moving about in a grass-lined runway will probably not detect a hawk or owl moving swiftly and silently above it until it is too late to escape. Habitat familiarity and the possibility for escape may play a role only if the avian predator has a significant chance of missing the vole on the first strike and then has to chase after the vole on foot. An avian predator using sound to locate prey can miss the prey if the prey suddenly stops moving (Konishi 1973). In this type of situation, young, inexperienced voles may do worse than

animals familiar with the habitat. Because mammalian predators, such as feral cats, actively pursue their prey, no prey class may be immune.

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