

## *Microtus* population biology: demography of *M. oregoni* in southwestern British Columbia

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Populations of *Microtus oregoni* were livetrapped from 1971 to 1974 in old field and grassland habitats at the University of British Columbia Research Forest, Maple Ridge, B.C. Forest (1974–1978) and shrub (1975–1980) habitats were also sampled intensively. An additional population was livetrapped (1971–1974) in abandoned grassland near Ladner, B.C. *Microtus oregoni* exhibited a 3–4 year cyclic fluctuation in abundance in the old field and shrub habitats. Maximum density (72 voles/ha) was recorded on the old field grid which was optimum habitat for this species. Winter breeding and a long reproductive period prior to the peak year, and larger body size during the peak than in other phases of the cycle were characteristic features of the old field population. This vole species did not have a multiannual cycle in habitats where the competitor, *M. townsendii*, was present. Oregon voles were 3–4 g heavier at the Research Forest than at the Ladner study area. Female voles were more prevalent than males in all populations.

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Des pièges permettant la capture d'animaux vivants ont été installés de 1971 à 1974 dans le territoire de populations de *Microtus oregoni* dans deux types d'habitat, champ abandonné et prairie, de la station de recherche de l'Université de Colombie Britannique, à Maple Ridge, C.B. Une forêt (1974–1978) et un bosquet de buissons (1975–1980) ont été échantillonnés également de façon intense. Des pièges ont servi aussi à échantillonner une population résidente d'une prairie abandonnée près de Ladner en Colombie Britannique (1971–1974). Les populations de *M. oregoni* subissent des fluctuations de densité selon un cycle de 3–4 ans dans le champ abandonné et le bosquet de buissons. La densité maximale (72 campagnols/ha) a été enregistrée dans le champ abandonné, habitat idéal de cette espèce. La population du champ abandonné se caractérise par sa reproduction en hiver et par sa période de reproduction particulièrement longue avant l'année de densité maximale et par la taille plus grande des individus durant l'année de densité maximale. Dans les habitats où *M. oregoni* cohabite avec son compétiteur *M. townsendii*, on n'observe pas de cycle multi-annuel. Les campagnols d'Oregon de la station de recherche de Maple Ridge sont plus lourds de 3–4 g que ceux de Ladner. Les femelles sont plus nombreuses que les mâles dans toutes les populations.

[Traduit par le journal]

### Introduction

Populations of microtine rodents fluctuate in regular cycles of abundance every 2 to 5 years (Krebs and Myers 1974). The majority of these vole species require a minimum level of vegetative cover to increase in numbers during multiannual population fluctuations (Birney et al. 1976). Grassland is the preferred habitat of the *Microtus* species which have been intensively studied.

The Oregon vole, *M. oregoni*, is widely distributed throughout the coastal forest habitats of the Pacific Northwest from extreme southern British Columbia to northern California (Banfield 1974). This vole occurs in forested areas but prefers the edges of timber and abandoned brushland (Goertz 1964). With the preponderance of cutover forest land, *M. oregoni* has been associated with various stages of postlogging succession (Gashwiler 1970, 1972; Hooven 1973a, 1973b;

Petticrew and Sadleir 1974; Hooven and Black 1976; Sullivan 1980).

*Microtus oregoni* populations have been studied in coastal forest and cutover habitats (Hawes 1975) and in abandoned farm land (Redfield et al. 1978). However, little information is available to determine the existence of multiannual population fluctuations for *M. oregoni* in optimum forest edge habitat. Tamarin (1977) has indicated that at least one species of *Microtus* (*M. breweri*) does not show population cycles.

This study was designed to analyze the periodicity of population fluctuations and related demographic parameters in *M. oregoni*. This information was derived from intensive monitoring of Oregon vole populations in old field, successional shrub, grassland, and forest habitats in southwestern British Columbia.

### Description of study areas

This study was located near Vancouver in the University of British Columbia Research Forest, Maple Ridge, B.C., and at the Ladner Air Base, 36 km southwest of Maple Ridge. At the Research Forest, trapping areas were located in forest, old field, and successional grassland and shrub cutover habitats

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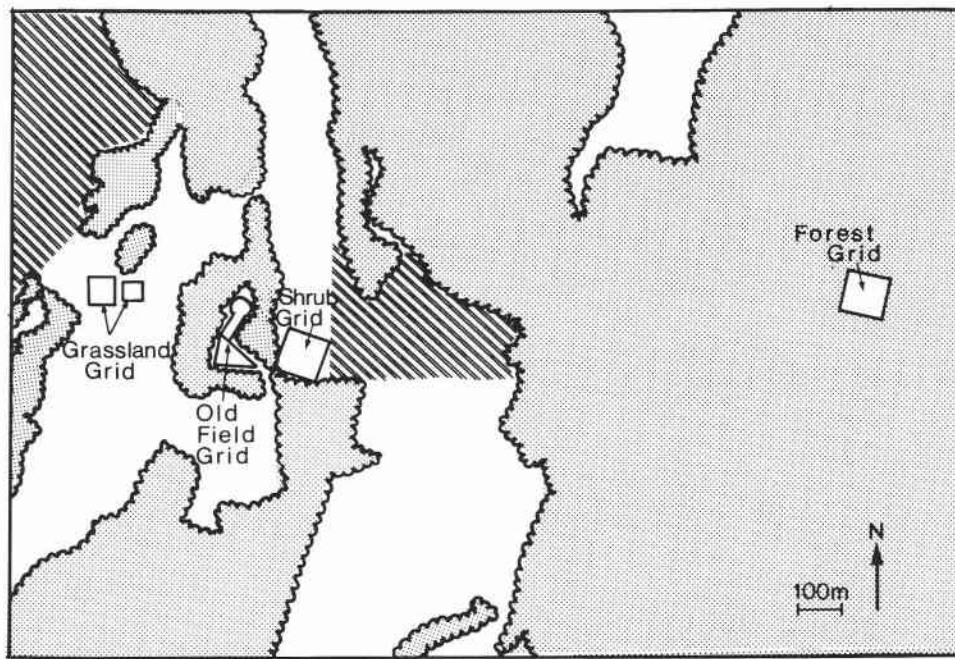


FIG. 1. Location of old field, grassland, shrub, and forest grids at the University of British Columbia Research Forest, Maple Ridge, B.C. Shaded areas represent forest and parallel-lined areas represent conifer plantations. Unshaded areas are grassland and (or) early successional cutovers.

(Fig. 1). The forest grid was operated in the southeastern part of the Research Forest. This habitat consisted of second-growth timber after a fire in 1925. Natural regeneration began between 1930 and 1932 and resulted in a forest 43 to 47 years old. This forest was dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and some Douglas fir (*Pseudotsuga menziesii*).

The old field habitat consisted of two abandoned fields on an old homestead and was surrounded by forest 70–90 years old. The old field grid (1.0 ha) was composed of the two contiguous fields. The grassland habitat was a 20-ha area that was logged and cleared in 1968, and subsequently seeded with natural grasses. Two grid areas (0.58 ha and 0.63 ha), essentially contiguous, were located on this grassland approximately 250 m from the old field grid.

The shrub grid was on an area (23 ha) logged in the autumn of 1973. Cover included slash with an abundance of deciduous trees and shrubs such as red alder (*Alnus rubra*), black raspberry (*Rubus leucodermis*), and salmonberry (*Rubus spectabilis*). Herbaceous annuals such as bracken (*Pteridium aquilinum*) and fireweed (*Epilobium angustifolium*) were also prevalent.

The Ladner grid (0.64 ha) was situated in the southwest corner of an old airport complex, about 100 m from Boundary Bay. This area lies in a matrix of several hundred hectares of grassland and was not subject to disturbances from local farming practices.

### Materials and methods

Each of the old field, grassland, and Ladner grids was

covered by a checkerboard of trap stations placed 7.6 m apart. One Longworth live trap was located at each station. The old field grid was irregularly shaped and had 173 stations. This grid was monitored every 2 weeks from May 1971 to June 1974. Snow prevented trapping for 6 weeks during the winter of 1971–1972. The grassland grid (two matrices  $9 \times 12$  and  $10 \times 10$ ) was trapped every 2 weeks from June 1972 to May 1974. The Ladner grid had 100 trap stations and was monitored every 2 weeks from May 1971 to November 1974.

The 1-ha checkerboard forest and shrub grids had 49 trap stations located at 15.2-m intervals with one Longworth trap per station. The forest grid was trapped biweekly from April to December 1974, March to November 1975, March to December 1976, March to November 1977, and March to September 1978. The shrub grid was monitored every 2 weeks from June to September 1975, April to October 1976, March to August 1977, March to November 1978; and every 3 weeks from May to November 1979, and April to November 1980.

Traps were baited with whole oats, and cotton was supplied as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods. All voles captured were weighed on spring balances, sexed, and ear tagged with serially numbered fingerling fish tags. Information on breeding performance was noted by palpation of male testes and noting condition of vaginal openings and mammarys of the females.

The estimates of density on the forest grid (1974–1978) and shrub grid (1975–1977) are minimum number of voles captured. All other grids and the shrub grid (1978–1980) are

TABLE 1. Trappability estimates for *Microtus oregoni* on the old field, grassland, and Ladner grids during summer (breeding) and winter (nonbreeding) periods of 1971 to 1974, and on the shrub grid during 1978 to 1980. Sample size in parentheses.

	Old field		Grassland		Ladner		Shrub Grid	
	Males	Females	Males	Females	Males	Females	Males	Females
Summer 1971	0.75(17)	0.73(47)	—	—	0.64(18)	0.61(45)		
Winter 1971–1972	0.95(8)	0.67(21)	—	—	0.77(7)	0.52(24)		
Summer 1972	0.79(28)	0.70(32)	1.00(2)	0.90(5)	0.56(9)	0.66(22)		
Winter 1972–1973	0.57(19)	0.55(24)	0.85(22)	0.85(21)	0.56(6)	0.55(20)		
Summer 1973	0.74(23)	0.64(57)	0.91(4)	0.70(10)	0.56(6)	0.68(23)		
Winter 1973–1974	0.62(22)	0.52(37)	0.84(11)	0.62(14)	0.71(6)	0.49(20)		
Summer 1974	0.76(18)	0.77(43)	0.95(5)	0.81(12)	0.56(6)	0.86(22)		
1978							0.73(16)	0.71(17)
1979							0.82(3)	0.63(3)
1980							0.86(7)	0.92(12)

minimum number known to be alive for each trapping period. Enumeration techniques provide sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught each sampling time (Hilborn et al. 1976).

Age-classes of animals were determined by body weight. Two age-classes of adults and juveniles (voles in juvenile and subadult age-classes pooled together) are referred to throughout the paper. Juveniles are considered to be young animals recruited during breeding seasons. Recruits are defined as new animals which enter the population.

Our data analysis is complicated because the same voles are captured in several sampling periods. Therefore, chi-square analyses have been utilized for data in which the samples are not completely independent. Examples are the proportion of animals in breeding condition, survival rates, and sex ratios. For this reason, the tests may not be statistically valid but are used as an indication of the degree of difference between sets of data.

In the appropriate figures and tables, each of the main grids is designated by a letter in the following manner: old field (A); grassland (B); and Ladner (C). The analysis of demographic parameters included these three grids since they represent synchronous sets of data.

## Results

### Trappability

The enumeration of voles in these populations is based on the assumption that most of the individuals in a given population are captured. The best estimate of trappability is the minimum unweighted calculation which eliminates first and last captures and hence all animals caught only once or twice (see Boonstra and Krebs 1978). Trappability estimates for the populations are given in Table 1. Trappability was generally high (averaging 72%) for all populations except during the winters of 1972–1973 and 1973–1974 (females) when this measure declines to less than 60% for voles on the old field and Ladner grids.

### Population density and recruitment

Population changes for the Oregon vole on the old field grid are illustrated in Fig. 2. Density of voles reached a peak of 46 animals in the fall of 1971 and 1972 with the majority of recruitment occurring during the breeding seasons. Overwinter abundance declined to 6 voles in 1971–1972 and to 15 animals in 1972–1973. The breeding season began prematurely in January 1973 coincident with very mild weather. Density reached a high of 72 voles in September 1973 and then declined overwinter to 32 animals during the start of the subsequent breeding season. The abundance of voles began increasing again until the end of the study in June 1974.

The population changes of *M. oregoni* on the forest and shrub grids are shown in Fig. 3. Voles were most frequently captured in the forest during 1974 and again in 1978. No more than two voles were caught during any given trapping period from 1975 to 1977. Since forest is not preferred habitat for Oregon voles, relatively high numbers during a given year may indicate a higher abundance of this species in more favourable areas. The successional shrub grid (Fig. 2) showed little variation in density during the first few years after logging (1975–1977). However, the population increased to 34 voles in the fall of 1978 and then declined dramatically overwinter. Numbers remained stable at 7 or 8 voles during 1979 before increasing to 20 animals in the fall of 1980.

The population density of voles on the grassland grid from 1972 to 1974 is illustrated in Fig. 4. There was little variation in abundance between years with the highest densities occurring in the fall of 1972 (33 voles) and 1973 (22 voles). This pattern contrasts with that occurring on the old field grid (only 250 m away) where *M. oregoni* reached an annual peak in abundance during the breeding season each year. It should be noted that

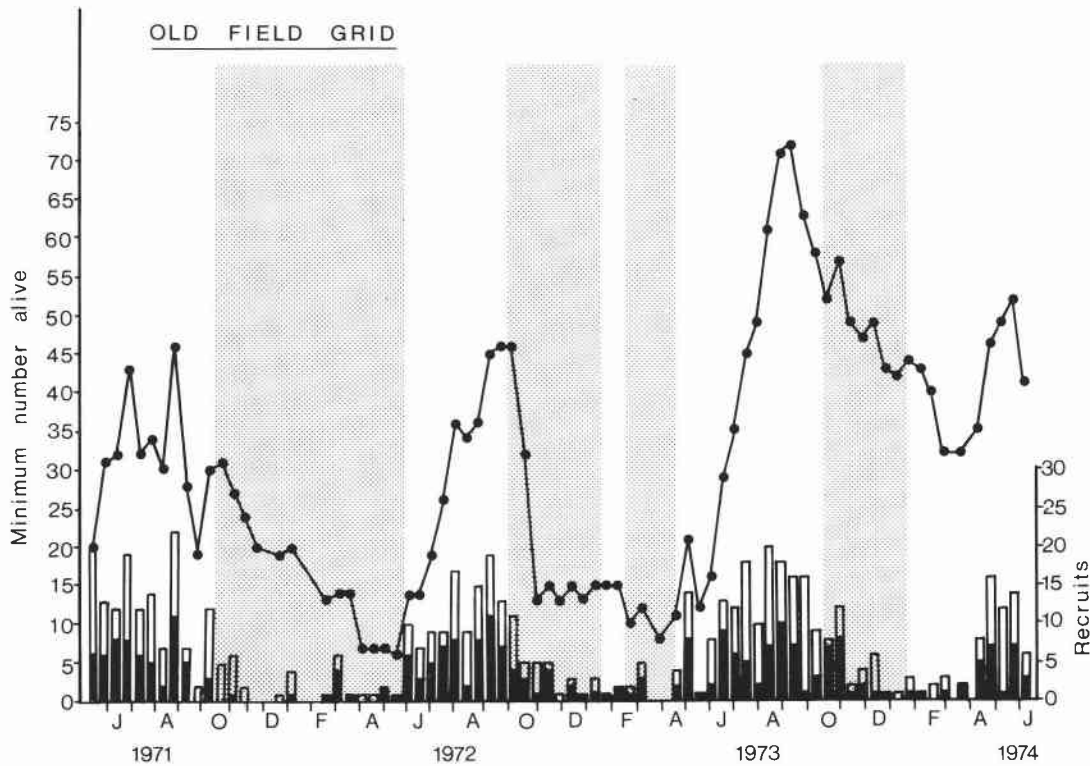


FIG. 2. Population density per hectare on the old field grid during 1971–1974, *Microtus oregoni*. Nonbreeding seasons are shaded. Histograms indicate number of new males (shaded) and females (unshaded) recruited into population.

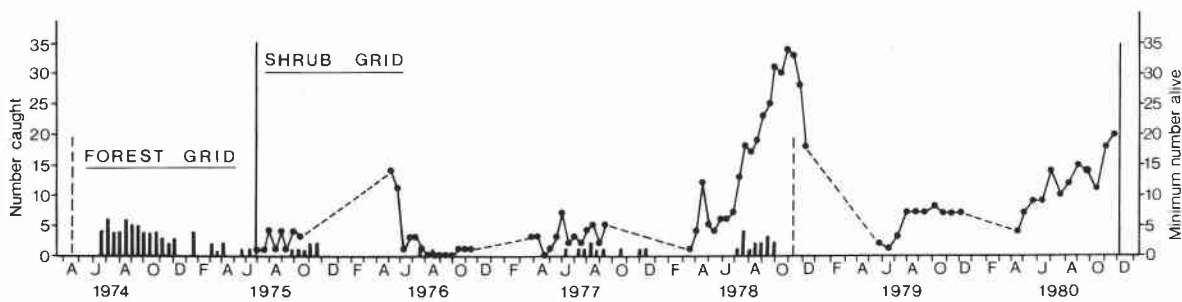


FIG. 3. Population density per hectare on forest grid (1974–1978) and shrub grid (1975–1980), *Microtus oregoni*. Shaded histograms represent number caught on forest grid (between vertical dotted bars). Closed circles represent number caught (1975–1977) and minimum number alive (1978–1980) on shrub grid (between solid vertical bars).

mixed populations of *M. oregoni* and *M. townsendii* occupied the grassland grid whereas an essentially "pure" population of the Oregon vole inhabited the old field grid. *Peromyscus maniculatus* was present at both areas as well as on the shrub and forest grids which is typical of its ubiquitous nature.

Population changes of *M. oregoni* living in an old field grassland at Ladner are shown in Fig. 5. After an initially high density (54 voles), this population showed little year to year variation with fall densities of 19–30

voles and spring breeding densities of 7 or 8 voles. This population went to extinction during 1975. *Microtus townsendii* was present at comparable densities throughout the study until fall 1974 when they increased dramatically.

#### Reproduction

The percentages of females with medium to large nipples and males with scrotal testes (50% levels) were used to determine the lengths of breeding seasons. The

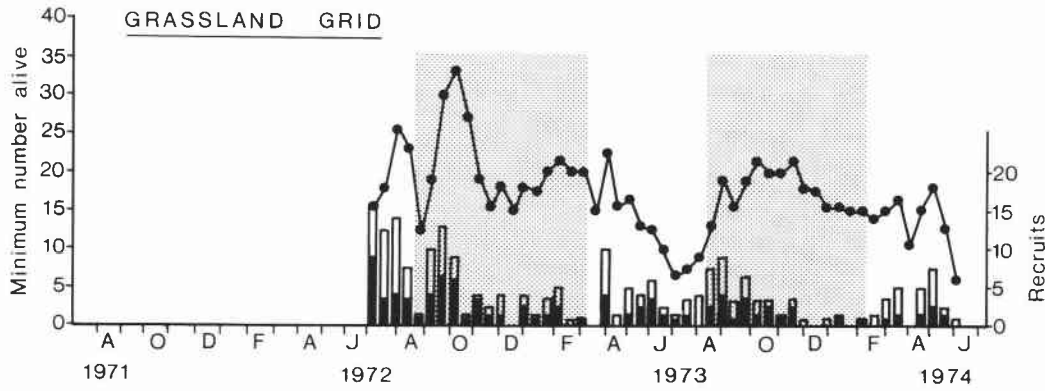


FIG. 4. Population density per hectare on grassland grid during 1972-1974, *Microtus oregoni*. Nonbreeding seasons are shaded. Histograms indicate number of new males (shaded) and females (unshaded) recruited into population.

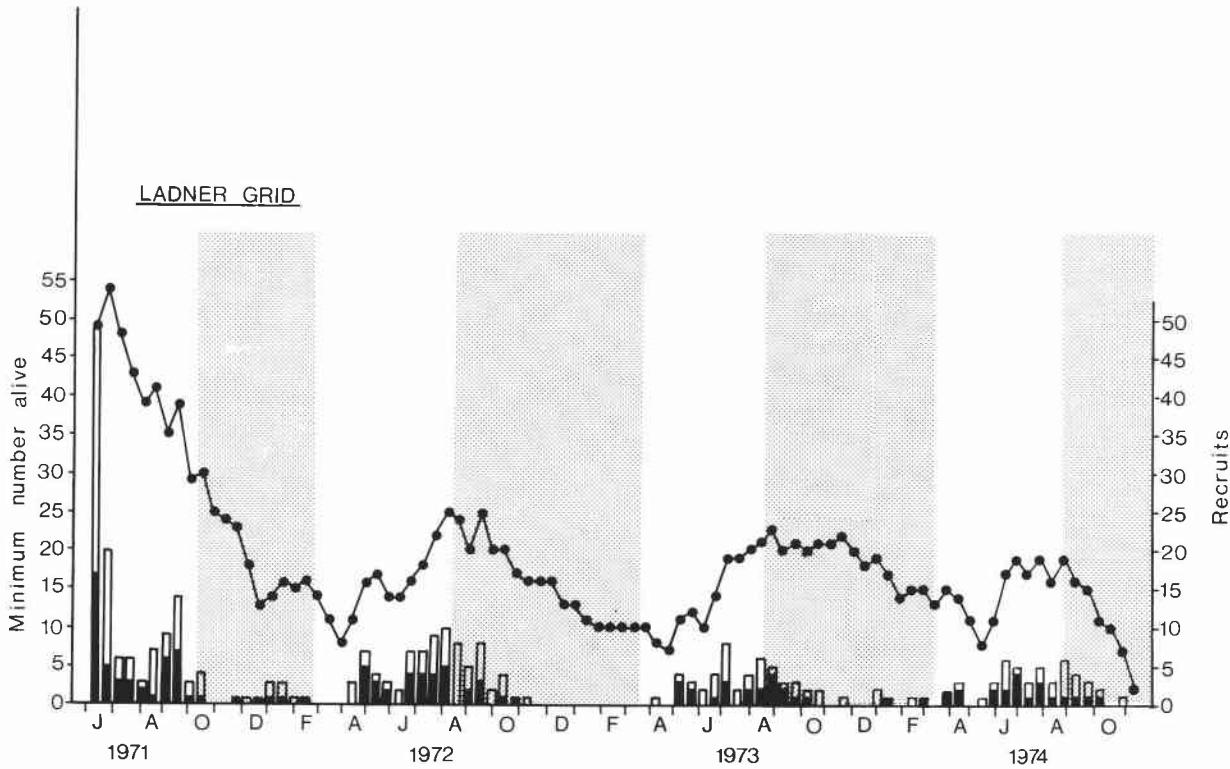


FIG. 5. Population density per 0.64 ha on the Ladner grid during 1971-1974, *Microtus oregoni*. Nonbreeding seasons are shaded. Histograms indicate number of new males (shaded) and females (unshaded) recruited into population.

relative lengths of these seasons are listed in Table 2. There were no consistent differences among any of the areas or years when comparing the lengths of complete breeding seasons. The longest breeding season on the old field grid was 1973 (25 weeks) which corresponds to the year of increase prior to the presumed population peak in 1974. In addition, breeding commenced in January during the winter of 1973-1974 (see Fig. 2).

Table 3 gives two measures of breeding performance

for the vole populations during their respective breeding seasons. There was no significant variation when comparing the proportion of breeding males between areas. However, significantly more adult females bred on the old field grid than at the Ladner area during 1971. This difference was reversed when comparing juvenile females on the two grids in 1971. More adult (1972) and juvenile (1974) females were breeding on the grassland grid than on the old field site. When analyzing the

TABLE 2. Length of breeding seasons (weeks) for *Microtus oregoni* on the three study areas during 1971 to 1974

	Old field	Grassland	Ladner
1971	21	—	17
1972	18	7+	22
1973	25	20	20
1974	20+	15+	22

variation between years for each study area, significantly fewer adult males were scrotal on the old field grid in 1974 than in either 1971 or 1973. This may be a result of the higher density of voles at the start of the 1974 breeding season than in previous years (see Fig. 2). The proportion of breeding adult females on the old field grid also showed a significant difference when comparing

1971 to each of the subsequent years. The proportion of reproductive animals showed little variation through time on the grassland. The high proportion of juvenile lactating females at Ladner in 1971 was significantly higher than any of the subsequent years. This incidence of breeding among smaller females may also have been caused by the higher density vole population during 1971 (see Fig. 4).

#### Mortality

Minimum survival rates for males and females in the three vole populations are given in Table 4. These average rates are summed over summer (breeding) and winter (nonbreeding) periods with an individual vole being tallied each time it is trapped. There were no consistently significant differences in male survival between years or study areas. However, female voles

TABLE 3. Proportion of *Microtus oregoni* in breeding condition on the three study areas during the breeding season of each year. Sample size in parentheses

Year and group	Old field (A)	Grassland (B)	Ladner (C)	Comparisons		
				A-B	A-C	B-C
1971						
Testes scrotal						
Adults	0.89(37) <i>i</i>	—	0.96(28)			
Juveniles	0.14(73)	—	0.24(29)			
Nipples large						
Adults	0.61(77) <i>abj</i>	—	0.36(74)		A-C**	
Juveniles	0.19(128) <i>cd</i>	—	0.45(60) <i>fgh</i>		A-C**	
1972						
Testes scrotal						
Adults	0.87(38)	0.92(13)	0.93(30)			
Juveniles	0.18(72)	0.35(20)	0.28(25)			
Nipples large						
Adults	0.27(48) <i>a</i>	0.54(24)	0.42(55)	A-B*		
Juveniles	0.10(88)	0.24(33)	0.13(40) <i>f</i>			
1973						
Testes scrotal						
Adults	0.92(50) <i>e</i>	1.00(34)	0.93(14)			
Juveniles	0.20(100)	0.31(16)	0.33(12)			
Nipples large						
Adults	0.39(158) <i>b</i>	0.44(50)	0.36(47)			
Juveniles	0.07(148) <i>c</i>	0.21(29)	0.10(48) <i>g</i>			
1974						
Testes scrotal						
Adults	0.69(64) <i>ei</i>	0.89(28)	0.85(13)			
Juveniles	0.31(32)	0.00(10)	0.22(18)			
Nipples large						
Adults	0.43(135) <i>j</i>	0.30(23)	0.32(84)			
Juveniles	0.04(118) <i>d</i>	0.18(39)	0.13(38) <i>h</i>	A-B*		

NOTE: Values with the same lower case designation are significantly different: *a-a*, *b-b*, *c-c*, *d-d*, *e-e*, *f-f*, *g-g*, *h-h* ( $p < 0.01$ ); *i-i*, *j-j* ( $p < 0.05$ ). Significant difference calculated by chi-square test.

TABLE 4. Minimum survival rates per 14 days for summer (breeding) and winter (nonbreeding) periods for the three study areas. Sample size is in parentheses

Season and group	Old field (A)	Grassland (B)	Ladner (C)	Comparisons		
				A-B	A-C	B-C
<i>Males</i>						
Summer 1971						
Total	0.53(96) <i>b</i>	—	0.59(81)			
Adults	0.71(34)	—	0.64(28)			
Juveniles	0.44(62)	—	0.57(53)			
Winter 1971-1972						
Total	0.66(53)	—	0.73(41)			
Summer 1972						
Total	0.60(88)	0.44(25)	0.60(50)			
Adults	0.70(33)	0.40(10)	0.63(30)			
Juveniles	0.55(55)	0.47(15)	0.55(20)			
Winter 1972-1973						
Total	0.55(95) <i>a</i>	0.75(142)	0.65(43)	A-B**		
Summer 1973						
Total	0.65(141)	0.51(59)	0.58(24)			
Adults	0.72(50)	0.58(45)	0.67(15)			
Juveniles	0.62(91)	0.29(14)	0.44(9)	A-B*		
Winter 1973-1974						
Total	0.76(90) <i>a</i>	0.75(84)	0.75(44)			
Summer 1974						
Total	0.70(92) <i>b</i>	0.64(42)	0.45(33)		A-C*	
Adults	0.76(59)	0.75(32)	0.73(15)			
Juveniles	0.58(33)	0.30(10)	0.22(18)		A-C*	
<i>Females</i>						
Summer 1971						
Total	0.71(180) <i>ch</i>	—	0.73(194) <i>fg</i>			
Adults	0.73(74)	—	0.75(88)			
Juveniles	0.69(106)	—	0.72(106)			
Winter 1971-1972						
Total	0.74(129) <i>j</i>	—	0.83(96)			
Summer 1972						
Total	0.69(127) <i>ei</i>	0.53(43)	0.76(89)			B-C*
Adults	0.78(45)	0.65(17)	0.81(52)			
Juveniles	0.63(82)	0.46(26)	0.70(37)			
Winter 1972-1973						
Total	0.60(95) <i>dj</i>	0.70(141)	0.77(128)		A-C**	
Summer 1973						
Total	0.79(278) <i>hi</i>	0.64(78)	0.85(86) <i>f</i>	A-B**		B-C**
Adults	0.84(152)	0.63(48)	0.91(43)	A-B**		B-C**
Juveniles	0.73(126)	0.67(30)	0.79(43)			
Winter 1973-1974						
Total	0.80(127) <i>d</i>	0.77(102)	0.87(120)			
Summer 1974						
Total	0.85(239) <i>ce</i>	0.63(68)	0.87(115) <i>g</i>	A-B**		B-C**
Adults	0.87(111)	0.58(26)	0.88(86)	A-B**		B-C**
Juveniles	0.82(128)	0.67(42)	0.83(29)			

NOTE: Values with the same lower case designation are significantly different: *a-a, c-c, d-d, e-e, f-f, g-g* ( $p < 0.01$ ); *b-b, h-h, i-i, j-j* ( $p < 0.05$ ). Significant difference calculated by chi-square test.

TABLE 5. Indices of early juvenile survival for the three populations. Ranges for indices of survival based on samples including two or more females. *N* = number of trapping weeks

	Old field			Grassland			Ladner		
	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range
1971	1.61	14	0.20–3.50	—	—	—	1.00	8	0.18–2.33
1972	4.15	11	1.67–5.67	2.24	8	0.33–4.67	2.20	14	1.00–3.00
1973	1.74	13	0.40–4.67	1.42	13	0.25–3.00	1.52	13	0.67–3.00
1974	1.62	6	1.25–2.00	2.60	5	0.00–0.50	1.06	14	0.00–2.50

generally survived better in the old field and Ladner populations compared with that in the grassland. This variation was statistically significant ( $p < 0.01$ ) during the summers of 1973 and 1974. Female survival was significantly higher during the later than the earlier years of the study on the old field and Ladner grids. There was little variation in female vole mortality in the grassland population.

Early juvenile survival may be measured by an index relating recruitment of young voles into the trappable population to the number of lactating females (Krebs 1966): index = no. of juvenile mice in week *t*/no. females with medium to large nipples caught in week *t* - 4. Table 5 gives the mean indices for the three populations during the breeding season and up to the end of recruitment of young. Survival of young voles was highest during 1972 on the old field (4.15) and Ladner (2.2) grids with little variation for this measure during the other years of the study. Juvenile survival was 2.24 in the grassland population during 1972 and increased to 2.6 in 1974. In general, survival averaged between one and two juveniles per lactating female on all areas.

#### Growth

The age categories of the voles and the body weights of male voles during breeding and nonbreeding periods are to be examined in this section. Owing to the lack of a better criterion, body weight must be used as an index of age. The percentage of sexually mature animals in a series of weight classes may be used to determine the weight limitations for juveniles and adults. The juvenile age-class includes both juveniles (seldom, if ever, sexually mature) and subadults (individuals of which < 50% are mature in the upper weight class) pooled together. Adults must have at least 50% of voles sexually mature in the lowest weight class. Using these criteria, the weight limits for age-classes for *M. oregoni* on the old field and grassland grids at the University Research Forest were the following: juveniles 1–20 g; adults  $\geq 21$  g; for the Ladner population: juveniles 1–17 g; adults  $\geq 18$  g.

Female body weights are complicated by undetected pregnancies and hence these data are more variable than that for males. Therefore, only mean body weights with

95% confidence limits for male *M. oregoni* are presented in Fig. 6. There was little difference in summer weights between adult males in the old field and grassland populations. However, grassland voles were significantly heavier than old field animals during the winter of 1972–1973. In general, Research Forest adult males were up to 4 g heavier than their counterparts at Ladner. Similarly, juvenile males were up to 3 g heavier on the old field and grassland grids than at Ladner.

A characteristic feature of cyclic populations of *Microtus* is the larger size (20–30%) of adult voles in peak populations than in other phases of the cycle (Krebs 1979; Boonstra and Krebs 1979). Table 6 gives the changes in spring body weights for the old field populations whose density changes were shown in Fig. 2. There was little difference in body size or spring densities between 1972 and 1973. However, male voles were up to 3.4 g heavier and the population density about three times higher in the spring of 1974 than in 1973.

#### Sex ratios

The sex ratios of the three populations have been

TABLE 6. Spring body weight distributions for male *Microtus oregoni* on the old field grid. Data are for individual males livetrapped during March and April of each year

Weight class (g)	Spring 1972	Spring 1973	Spring 1974
10–12	0	1	0
12–14	0	3	1
14–16	0	0	1
16–18	1	1	0
18–20	2	2	0
20–22	5	0	3
22–24	3	2	2
24–26	2	2	7
26–28	0	1	2
28–30	0	0	1
30+	0	0	0
Average body weight	20.8	18.4	22.8
<i>n</i>	13	12	17



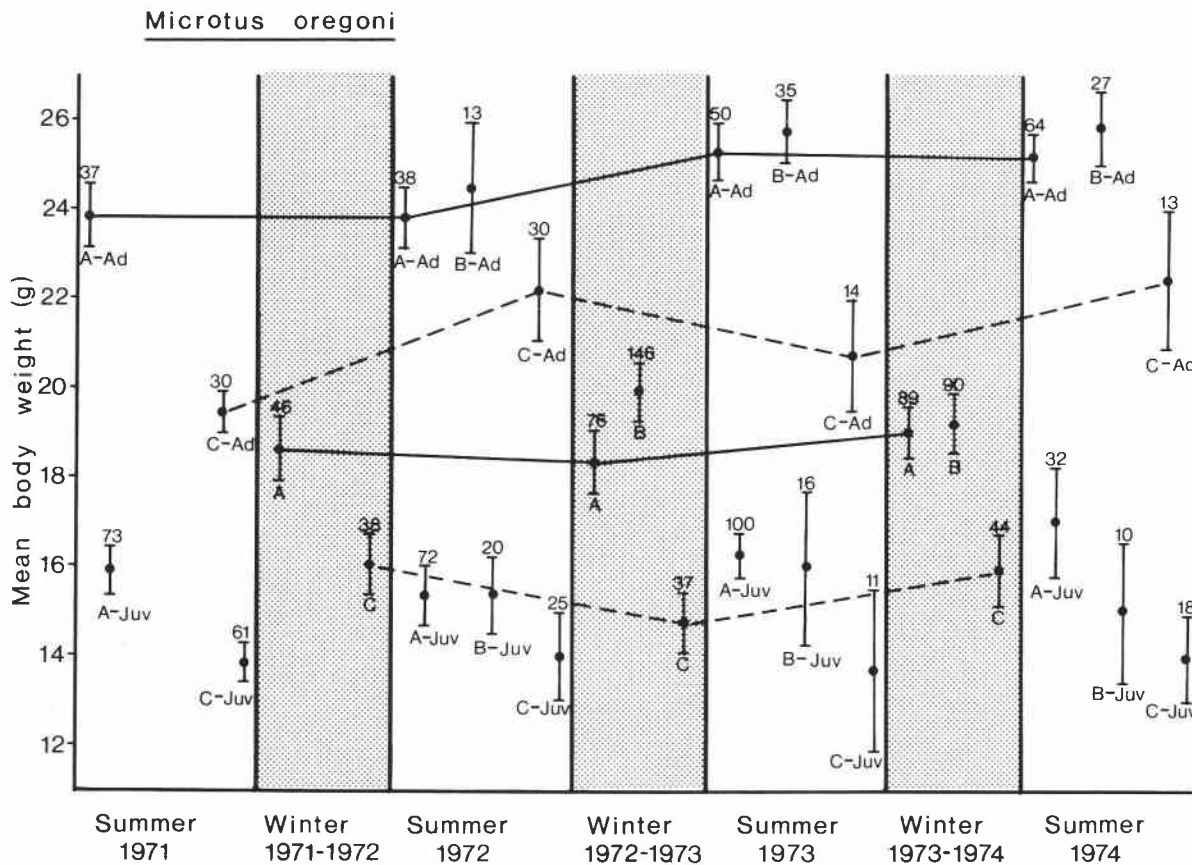


FIG. 6. Mean body weights of male *Microtus oregoni* from the old field (A), grassland (B), and Ladner (C) populations during 1971–1974. Data are grouped over the summer (breeding) and winter (nonbreeding) periods. Vertical bars represent 95% confidence limits. Sample size above upper confidence limits. Ad, adult; Juv, juvenile.

estimated from the minimum number known to be alive and these data have been summed for each year of the study. The proportion of males and statistical comparisons for each population are listed in Table 7. The grassland sex ratio stayed relatively constant throughout the study whereas the other populations varied from one year to another. There were significantly more males in

the grassland than old field and Ladner populations, and the old field population had more males than at Ladner. In general, female voles were more prevalent than males in these populations.

### Discussion

Populations of *M. oregoni* have been intensively monitored in old field, grassland, successional cutover, and forest habitats. In addition, these areas have been compared with abandoned farmland (Ladner) which was not associated with coastal coniferous forest. The Oregon vole prefers forest edges and brushland (Goertz 1964) and is frequently encountered on cutover forest lands. We conclude from our study that old field habitat in association with coniferous forest is optimum for populations of *M. oregoni*. This abandoned farmland was undergoing succession to coniferous and deciduous trees but at a much slower rate than is typical of coastal logged areas. Therefore, the old field was able to sustain a higher population of voles (up to 72/ha) than any other habitat and showed the tendency to cycle, at what might

TABLE 7. Sex ratios (proportion of males) for the three populations of *Microtus oregoni* in 1971 to 1974. Sample size in parentheses

Year	Old field	Grassland	Ladner
1971	0.30 (466) <i>a</i>	—	0.27 (519) <i>ef</i>
1972	0.42 (505) <i>abc</i>	0.46 (349)	0.27 (434) <i>g</i>
1973	0.36 (915) <i>cd</i>	0.43 (505)	0.21 (401) <i>e</i>
1974	0.29 (456) <i>bd</i>	0.39 (183)	0.19 (188) <i>fg</i>
Mean	0.35 (2342)**	0.43 (1037)**	0.25 (1542)**

NOTE: Values with the same lower case designation are significantly different: *a-a*, *b-b*, \*\* ( $p < 0.01$ ); *c-c*, *d-d*, *e-e*, *f-f*, *g-g*, ( $p < 0.05$ ). Significant difference calculated by chi-square test.

have been a 4-year interval, if the study had continued into the fall of 1974 and spring of 1975 on that area.

The forest grid had the highest number of captures of *M. oregoni* in 1974 and 1978. The first year (1974) corresponds to a presumed peak (see Figs. 2 and 3) and 1978 corresponds to a peak year on the shrub grid (Fig. 3). These results support the premise that *M. oregoni* cycles every 4 years. Hawes (1975) found little yearly difference in density of Oregon voles in hemlock forest and regrowth at the Research Forest (1971–1974). However, he did report slightly increased abundance in 1973 in the successional habitat before *M. townsendii* invaded the area and *M. oregoni* subsequently declined. This lack of cycling was similar to our grassland and Ladner study areas, both of which had resident populations of *M. townsendii*. Both populations of *M. townsendii* and *M. oregoni* declined on the grassland grid during the summer of 1973 possibly because of very dry weather (Hilborn and Krebs 1976). The old field and shrub grids had only *M. oregoni* and *P. maniculatus* populations.

The early (up to 4 or 5 years after logging) successional stages of cutovers provide suitable habitat for the Oregon vole. Studies on cutover forest land have indicated that this vole species may have a 3–4 year cycle in abundance (Gashwiler 1970, 1972; Petticrew and Saddleir 1974; Hooven and Black 1976). After an initial increase 4 years after logging, Gashwiler (1972) reported no consistent relationship between the age of a cutover and the density of *M. oregoni*. Therefore, the quality of habitat as determined by successional stage appears to be important for generating cycles in populations of Oregon voles. This relationship correlating food and cover with cycles of *Microtus* has been discussed by Birney et al. (1976).

Old field habitat at Ladner did not support a cycling population of *M. oregoni*. This was probably a result of competition from *M. townsendii* (which dominates *M. oregoni*; Hawes 1975) and isolation from coniferous forest habitats where *M. oregoni* most frequently occurs (Goertz 1964). Similarly, Oregon voles did not cycle in the grassland adjacent to the old field habitat. This grassland was successional and also had resident *M. townsendii*. Thus, it was not suitable to generate a cycling population of *M. oregoni*. The population of Oregon voles on the shrub grid did cycle, possibly because there were no *M. townsendii* there.

The variation in body weight (3–4 g difference) of Oregon voles between the Research Forest and Ladner was similar to that recorded by Hawes (1975). The more robust body size of voles at the Research Forest is probably associated with the coastal forest environment because there were similar body weights in old field and grassland populations. Since comparable densities of *M. townsendii* occupied the grassland (see Hilborn and

Krebs 1976) and Ladner (see Krebs et al. 1976) grids, their presence did not result in smaller size *M. oregoni* in the grassland population. Hawes (1975) concluded that the small size of Ladner *M. oregoni* was probably genetically rather than environmentally induced and we concur with this conclusion. Oregon voles do occupy the Douglas fir forests which are remotely associated with the general Ladner area (Hawes 1975; Taitt 1978), but no information is available on body weights.

There was a preponderance of female Oregon voles in the three populations in this study. The lower average proportion of males varied from 0.25 (Ladner) to 0.35 (old field) to 0.43 (grassland). These results are quite different from the sex ratio of 54% males reported by Cowan and Arsenault (1954) and 47% males reported by Gashwiler (1972). The latter author has suggested that since it is difficult to sex young Oregon voles, errors could be made with live animals. However, if this was the case, then there should not have been the significant variation among our three study areas. Stenseth (1978) has suggested that a female biased sex ratio in wood lemmings (*Myopus schisticolor*) is maintained by cyclic inbreeding. This is a possible explanation for the generally high preponderance of females in populations of *M. oregoni*.

Thus, we conclude from this study that *M. oregoni* has a 3–4 year population cycle in old field habitat associated with coniferous forest. This vole may also cycle in some successional cutover habitats when a competitor, *M. townsendii* is not present. Other characteristic features of cyclic populations such as winter breeding and long breeding season prior to a peak population, with larger body size at the peak than in other phases of the cycle, tend to support our conclusion.

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