Some aspects of reproduction in the vole *Microtus townsendii*

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Changes in various reproductive parameters have pronounced effects on microtine population fluctuations. This study presents a detailed account of reproduction in *Microtus townsendii*. Populations in two areas were studied. On Westham Island, litter size, estimated by autopsy, was correlated positively with weight. There was no significant difference in litter size between primiparous and multiparous females. Females pregnant in spring had more embryos than those pregnant in summer or fall. Breeding was concentrated in spring and summer, with most females continuously pregnant.

In the University of British Columbia Research Forest, litter size at recruitment was found to be unrelated to parity, size, or LAP genotype of the mother. While the size of consecutive litters (determined by autopsy) was significantly repeatable within an individual mother, recruitment litter size was not. Autopsy litter size, as at Westham Island, was largest in spring, but recruitment litter size was largest in autumn. Entire litters were lost most often during winter and summer. Overnight trapping may be responsible for loss of some litters at or just before parturition. Litters born in traps were usually unsuccessful, but otherwise mothers of totally unsuccessful litters seemed to avoid traps. Neither parity nor LAP genotype was related to the loss of entire litters.

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Les variations de plusieurs paramètres relatifs à la reproduction ont des effets marqués sur les fluctuations des populations de microtinés. On trouvera ici le rapport d'une étude détaillée de la reproduction de *Microtus townsendii*, dans laquelle les populations de deux régions ont été étudiées. Chez les souris de l'île Westham, le nombre de petits dans la portée, estimé par autopsie, est proportionnel au poids. Il n'y a pas de différence significative entre les femelles primipares et les femelles multipares en ce qui concerne le nombre de petits dans une portée. Les femelles gravides au printemps portent plus d'embryons que les femelles enceintes à l'été ou à l'automne. La reproduction se fait surtout au printemps et à l'été, la plupart des femelles étant enceintes de façon continue.

Dans la forêt expérimentale de l'Université de Colombie Britannique, le nombre de petits par portée au moment du recrutement est indépendant du nombre de grossesses, du poids ou du génotype LAP de la mère. Bien que le nombre de petits dans une portée soit relativement stable chez le même individu (tel que le révèle l'autopsie), le nombre de petits dans une portée au moment du recrutement est variable. Comme dans l'île Westham, le nombre de petits dans une portée (déterminé par autopsie), est plus élevé à l'automne. C'est durant l'hiver et durant l'été qu'on assiste le plus fréquemment à la perte de portées entières. Le piégeage la nuit au moment de la parturition ou juste avant est peut-être responsable de la perte de quelques portées. Les portées nées dans les pièges ne survivent ordinairement pas; par ailleurs, les mères de portées qui ne survivent pas du tout semblent échapper au piégeage. Ni le nombre de grossesses, ni le génotype LAP ne sont reliés à la perte totale des petits.

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Introduction

Reproduction in rodents of the genus *Microtus* is particularly important because of its role in their population dynamics. During a typical cyclic fluctuation of a *Microtus* population, two specific aspects of reproduction appear to be major components of changes in numbers: length of breeding season, and age at sexual maturity. Some aspects

appear to be unrelated to population fluctuations: litter size (as measured by embryo counts), proportion of the population reproducing, and sex ratio (Krebs and Myers 1974). Other aspects may well be important, but have been hard to measure in trapping studies: survival of nestlings, and the distribution of reproductive effort and success among individual females and among genotypically different animals. In this paper we examine a number of aspects of reproduction, including some in this last category, for two populations of *M. townsendii* in British Columbia. We find the problems of nestling survival and reproductive effort by individual

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females particularly interesting, as they are important components of the fitness of a female vole and hence may play a major role in determining the genetic structure of a population.

There is little information in the published literature about the process of reproduction in *M. townsendii* (Hasler 1975; Cowan and Guiguet 1973). Therefore, it is useful to collect a profile of reproduction parameters for this species, to provide a basis for comparison with others. Like other microtines, *M. townsendii* exhibits marked population fluctuations. Though these fluctuations appear to be irregular instead of every 2–4 years as they occur in most species of *Microtus*, they share many of the demographic attributes of the more typical population "cycles" (LeDuc and Krebs 1975). The data presented here characterize two populations which differ dramatically in the habitats they occupy and thus provide evidence of the flexibility with which this species adjusts its reproduction to its environment.

Methods

The animals used in this study came from two separate populations; one study area was located in river delta grassland on Westham Island near Vancouver, B.C., and the other area was located on a hillside sown with grass after removal of a Douglas fir forest, in the University of British Columbia (U.B.C.) Research Forest at Haney, B.C. Grass dominated the vegetation on the Westham Island site, accounting for more than 90% of the cover. The most common grass species, in decreasing order of abundance, were *Agrostis alba*, *Agropyron repens*, *Poa pratensis*, and *Holcus lanatus*. Few herbaceous species were found; the most common was creeping thistle, (*Cirsium arvense*). Grass was less abundant at the U.B.C. Research Forest site, accounting for about 60% of the vegetative cover. Because it had a south-facing exposure, this site became very dry in the summer whereas the other site remained moderately moist. The most common grass species, in decreasing order of abundance, were *Festuca rubra*, *Agrostis tenuis*, *Dactylus glomerata*, *Agrostis alba*, and *Phleum pratensis*. A rush species, *Juncus effusus* var. *pacificus* accounted for about 20% of the vegetative cover and was abundant along water drainages. Shrubs and herbs were more common here than at the Westham Island site; among the more frequent were *Epilobium angustifolium*, *Anaphalis margaritacea*, *Polystichum munitum*, *Rubus ursinus*, and *Alnus rubra*.

The females from Westham Island were collected from February 1973 to August 1974 on several trapping grids on which cropping experiments were being performed (Boonstra 1976). All specimens were autopsied, and the following were recorded: weight, lactation in progress, number of placental scars, number of live and resorbing embryos, and, in the animals collected from September 1973 to August 1974, the weight of uterus plus embryos. Females were considered nulliparous if no embryos, placental scars, or lactation were present, primiparous if there was evidence of only one pregnancy (either embryos alone or one set of scars), and multiparous if more than one set of scars, or scars plus embryos were present.

As part of a quantitative genetics study in the Research Forest study area, small enclosures (6 m × 6 m) confined pairs of animals in the natural habitat. The enclosures consisted of

hardware cloth buried 50 cm in the ground to prevent burrowing out, with a horizontal aluminum flange atop the fence so the voles could not climb out. Movement of voles between the pens was rare. One male and one female vole were introduced into each enclosure, and as they could not be observed directly once inside, their presence and reproductive condition were monitored by weekly overnight trapping with four Longworth traps per enclosure. Whenever possible, the male was removed from the enclosure before the birth of a litter and returned only after the young were removed at or soon after their first capture. Sixteen such enclosures were utilized from November 1972 through August 1974. During the winter (December–March) laboratory mouse chow was provided to supplement the limited supply of grass in the enclosures. Blood samples were taken from all Research Forest animals so they could be typed for the polymorphic locus leucine aminopeptidase (LAP), as described in LeDuc and Krebs (1975).

In addition to the small enclosures, one unfenced and two fenced grids (each about 0.8 ha) were trapped in adjacent habitat at the Research Forest, with a trapping regime similar to that employed on Westham Island. No food was added to these grids.

Most offspring first entered traps at about 3 weeks of age, though some took as long as 5 weeks, in the small enclosures. Under the trapping regimes employed on the larger grids at Haney and Westham Island, *Microtus townsendii* young are heavier by 10 g on the average when they first enter Longworth traps, compared with those in the small enclosures. Hence, we conclude that we sampled this species at a younger age than had been possible otherwise.

Repeatability (R) of litter size for individual females was estimated for embryo and scar counts using the following standard formula (Becker 1967):

$$R = s^2_B / s^2_T$$

where s^2_B is the between-individual component of variance and s^2_T is the total variance for repeated measurements.

Results

The Westham Island Population

Maternal Weight and Litter Size

The number of embryos per litter may vary with maternal body size, parity, season, and phase of the population cycle (Kalela 1957; Keller and Krebs 1970). In this study there was a significant correlation between maternal body weight and the number of visible embryos ($r = 0.20$, $N = 278$, $p < 0.001$). Weights of females were corrected for embryo weight by subtracting the weight of the gravid uterus from the total body weight. In the following analysis, only data obtained from September 1973 to August 1974 were used because gravid uterus weights were not recorded in earlier samples.

Parity and Litter Size

In some other species of microtines, primiparous females have smaller litters than do multiparous females (Hasler 1975). To examine whether parity in *M. townsendii* affected litter size, we performed an analysis of covariance on the two regression lines for primiparous and multiparous females in each of the three seasons: fall 1973, spring 1974,

TABLE 1. Linear regression analysis of living embryos vs. maternal body weight in *Microtus townsendii* at Westham Island. Primiparous and multiparous females were combined. *T* represents the test of the hypothesis that the regression slope is 0

Season	N	Mean embryo count	SE	Mean body weight, g	SE	Slope	SE	<i>T</i>	Intercept
Fall 1973	66	4.96	1.19	49.91	7.06	0.021	0.022	0.95	4.78
Spring 1974	92	5.42	1.12	48.67	8.88	0.048	0.013	3.69**	2.32
Summer 1974	120	4.92	1.00	53.15	7.90	0.034	0.011	3.09*	2.77
Pooled	278	5.10	1.10	50.89	8.29	0.027	0.008	3.53**	3.70

NOTE: *, $p < 0.01$; **, $p < 0.001$.

TABLE 2. Mean living embryo counts for *Microtus townsendii* at Westham Island, by season. Primiparous and multiparous females were pooled. Adjusted means utilized the regression equations in Table 2 to estimate the embryo count for a 51-g female

Season	N	Mean embryo count	SE	Adjusted mean embryo count	SE	95% confidence limits
Spring 1974	92	5.42	0.12	5.50	0.11	5.28–5.72
Summer 1974	120	4.92	0.09	4.83	0.10	4.64–5.02
Fall 1973	66	4.96	0.15	4.99	0.13	4.72–5.26

and summer 1974. No breeding occurred in winter. There was no effect of parity on litter size in any season nor on the pooled results ($F = 0.77$, $df = 1$, 271).

Season and Litter Size

Since litter size is influenced by maternal body weight but not by parity, we pooled primiparous and multiparous females within each season and performed an analysis of covariance to test for differences between seasons using the program BMD:10V. The linear regression for each of the seasons is given in Table 1, but only in the spring and summer of 1974 are the regressions significant. There was a significant difference in the adjusted mean embryo count between seasons (Duncan's multiple range test; $F = 9.98$, $df = 2$, 271), such that litters born in spring were larger than either fall or summer litters, which did not differ significantly from one another (Table 2).

Pregnancy Rate

The percentage of mature females which are pregnant during the breeding season is an important component of reproduction in microtine populations. In most *Microtus* species, the gestation period is 21 days, the embryos can be detected only from the 6th day onwards, and females can undergo postpartum estrus (Hoffman 1958; Hasler 1975). Therefore, a theoretical maximum pregnancy rate of 71% could be detectable by autopsy if all females were pregnant all the time. Keller and Krebs (1970) discuss the problems associated with determining pregnancy rate, one of which is how to decide whether females are sexually mature or not. We have chosen to consider all females 43 g or larger as

potentially mature (Krebs *et al.* 1976; LeDuc and Krebs 1975). Table 3 shows the estimated pregnancy rates for mature females for six time periods. There was no significant difference between the pregnancy rates of the two spring–summer breeding periods included in the study. The very high pregnancy rates for these periods indicate that almost all females were continuously pregnant. Breeding did not start or stop synchronously in all females and therefore we have partitioned those portions of the breeding season into transition periods. During the transition periods in late winter (February–March) and fall (October–November) fewer females were found to be pregnant. In December and January, no animals were found to be pregnant in this particular year.

The Research Forest Population

The breeding enclosures enable us to study some of the aspects of reproduction which have been difficult to approach through livetrapping studies or autopsies.

Litter Size at Recruitment

First, we were able to measure litter size for individual females at the point when the young first are recruited into the trappable population. Offspring of this age are the end products of the mother's reproductive effort and have a good start towards their own sexual maturity. Therefore, their numbers may be an important component of the mother's individual fitness.

Frequency distributions—Table 4 shows the frequency distributions of litter size during pregnancy (measured from embryo counts sampled

TABLE 3. Visible pregnancy rate for Westham Island based on the assumption that all females heavier than 43 g were sexually mature

Time period	No. nulliparous	No. not pregnant (primiparous or multiparous)	No. pregnant	Total	% of total pregnant
Later winter 1973	5	1	0	6	0.0
Spring, summer 1973	4	21	60	85	70.6
Fall 1973	11	36	28	75	37.3
Winter 1973	2	1	0	3	0.0
Late winter 1974	4	6	8	18	44.4
Spring, summer 1974	25	94	188	307	61.2

TABLE 4. Frequency distribution of litter sizes from autopsies of Research Forest females and recruits born in the breeding enclosures. Percentages of totals are given in parentheses

	Litter sizes							
	1	2	3	4	5	6	7	
Autopsies	0 (0.0)	2 (2.8)	6 (8.4)	16 (23.2)	25 (36.2)	14 (20.3)	6 (8.7)	$N = 69$, Mean = 4.88, SE = 1.18
Recruits from enclosures	9 (14.3)	12 (19.0)	8 (12.7)	10 (15.9)	15 (23.8)	5 (7.9)	4 (6.3)	$N = 63$, Mean = 3.65, SE = 1.80

during spring and summer, 1974, at the Research Forest) and at recruitment (counts from all enclosure litters with at least one young surviving to enter traps). The distributions are significantly different ($G = 21.16$, $p < 0.005$), and while the mean litter size at recruitment is smaller than that *in utero* ($t' = 4.61$, $p < 0.001$), the variance is significantly larger ($F = 2.32$, $df = 62, 68$, $p < 0.005$). Thus, since mean litter size at recruitment is only about 75% of that before birth, we may conclude that at least 25% of the young born are lost before they enter traps. In addition, we note that it is litters of average size which are most seriously affected, with the largest litters still fairly well represented at recruitment.

Repeatability—The estimate of repeatability for litter size during pregnancy was made from autopsy data in which two sets of scars of clearly different age, or embryos in addition to scars, were visible: $R = 0.479$, $SE = 0.165$, $N = 20$. The estimate of the repeatability of litter size at recruitment was calculated from breeding enclosure mothers which produced more than one litter: $R = -0.046$, $SE = 0.146$, $N = 14$. The difference in R at the two stages could be interpreted to mean that the female has some phenotypic or genotypic control over the number of embryos she produces, but relatively little control over the events or conditions which determine how many of her young will reach trappable age in this experimental setup.

Parity and size of mother—While embryo counts

are closely related to maternal weight in *M. townsendii*, and to parity in other species (Hasler 1975), litter size at recruitment appears to be unrelated to either maternal body size or parity. Among females raising litters in the enclosures, mean recruited litter size for primiparae was 3.77 ($SE = 1.90$, $N = 13$) and that for multiparae was 3.62 ($SE = 1.90$, $N = 39$). Zygomatic breadth was used as an indicator of body size in the breeding enclosure females; it is closely correlated with both body length and nonpregnant weight (Anderson 1975). There was no significant correlation between recruited litter size and zygomatic breadth of the mother ($r = -0.119$, $N = 60$, $p > 0.05$). Thus, even though large females have an apparent slight advantage with respect to the number of embryos they produce, they are unable to maintain that fitness advantage into the next generation. Thus body size does not seem to influence directly the component of fitness associated with reproductive output.

LAP genotype—The LAP locus appears to be associated with several reproductive parameters in the Westham Island population (LeDuc and Krebs 1975). However, females of all three LAP genotypes showed the same frequency distribution of recruited litter size ($\chi^2 = 2.408$, $df = 4$, $p > 0.5$).

Season of birth—Like the embryo counts of *M. townsendii* and other species (Hoffman 1958; Kott and Robinson 1963; Keller and Krebs 1970; Krebs and Myers 1974; Christian 1971), mean litter size at

recruitment varied with season of birth. However, the pattern of change in litter size at recruitment in the Research Forest differed from the pattern for embryo counts on Westham Island; at the Research Forest the largest mean litter size occurred in the autumn (Table 5), and breeding continued at a low level throughout winter (both with supplemental food in the small enclosures and without it on the adjacent large grids). Embryo counts (uncorrected for maternal body size) from the Research Forest population are available only for spring and summer (mean count = 4.66, $N = 29$ for summer; mean = 5.13, $N = 30$ for spring), but they change in a fashion similar to those from Westham Island. This result suggests the question, is the autumn peak in recruited litter size at the Research Forest a function of greater numbers of embryos, better survival of nestlings, or both? Data on overall success of litters help to answer this question partially.

Overall Litter Success

Another new kind of information available from the breeding enclosures was a picture of the risk taken by an individual mother of the loss of her entire litter. We categorized as 'successful' a litter from which at least one offspring entered the traps; whereas the litter was 'unsuccessful' if the mother was visibly pregnant, parturient, or lactating, but no young appeared in the traps subsequently. A large number of the detected pregnancies were unsuccessful: 44 out of 107 in the breeding enclosures, or 41%. This percentage is probably an underestimate, for it does not include litters resorbed at an early stage of the pregnancy, nor those cases in which signs of reproductive activity were missed. We examined several factors which might influence the incidence of unsuccessful litters.

Season of birth—The data in Table 6 supplement those in Table 5 and may indicate one reason why litter size at recruitment is high in autumn. Insofar as those factors which cause the loss of entire litters coincide with those causing the loss of part of a litter, Table 6 suggests that nestling survival is indeed high in both spring and autumn, relative to that in winter and summer, and thus may be a factor in the large size at recruitment of litters born between October and December.

TABLE 5. Recruited litter size vs. season of birth, pooled over years. $F = 4.615$, $p < 0.01$

Season of birth	Mean litter size	N
January–March	3.36	11
April–June	3.52	25
July–September	2.40	10
October–December	4.76	17

TABLE 6. Frequency distribution of successful and unsuccessful litters associated with season of birth, pooled over years. $\chi^2 = 6.33$, $df = 3$, $0.05 < p < 0.10$, $N = 107$

Season of birth	No. successful litters	No. unsuccessful litters
January–March	11	15
April–June	25	10
July–September	10	10
October–December	17	9

Stage of failure—Table 7 shows the frequency distribution of the stages of the reproductive process at which the litters apparently failed, i.e., the last reproductive activity seen in the mother during the supposed period of pregnancy and lactation for that litter. Though this table suggests that late pregnancy and parturition are the most hazardous time for the litter, several considerations modify this conclusion. First, lactation is more demanding on the energy reserves of the mother than is pregnancy (Sadleir 1969a, 1969b). In this study, too, mothers of unsuccessful litters disappeared (and presumably died) more frequently during lactation than during pregnancy. Finally, it seems likely that mothers trapped near the time of parturition may abort or resorb their litters. One indication of this problem is described in "Effects of trapping" below.

Effects of trapping—At least some of the litter failures are attributable directly to the effects of trapping. Only 1 litter of 8 litters born in traps was successful compared with 62 out of 97 born outside traps ($p = 0.008$, Fisher exact test). Thus we see that litters actually born in live traps are almost always unsuccessful, even when they are not cannibalized by their mothers. Thus, for an undisturbed population, we must revise downward the estimate for the proportion of unsuccessful litters (41%) because no litters would be lost in traps. Such an estimate would be 37 of 107, or 35% unsuccessful litters. Because the enclosures may have protected litters from other sources of mortality, this is probably a minimum estimate for an undisturbed population.

In contrast, mothers of successful litters are generally more trappable than those of unsuccessful litters. To obtain data for this analysis, we tallied the number of trap nights and number of captures for the period of late pregnancy to weaning for successful litters, and late pregnancy to last visible sign of reproduction for mothers of unsuccessful litters. Only mothers exposed to more than one trap night during the vulnerable period were included in the analysis. Females producing successful litters

TABLE 7. Frequency distribution of stage of failure of unsuccessful litters. $N = 44$

Last stage observed	No. failures	%
Late pregnancy, parturition	30	68.2
Lactation, week 1	6	13.6
Lactation, week 2	4	9.1
Lactation, week 3	4	9.1

were caught on 76% of the possible trap nights ($N = 169$) compared with 50% ($N = 28$) of the females producing unsuccessful litters ($\chi^2 = 7.91, p < 0.01$).

Distribution among individual females—Sufficient females in the enclosures produced two or three litters to make possible a test for random distribution of litter success among females. The observed frequency distributions were compared with the expected values under the null hypothesis that successful and unsuccessful litters were distributed binomially among females. The null hypothesis was accepted. (Kolmogorov-Smirnov test; $N = 19$ for mothers with two litters, and $N = 9$ for those with three litters; $p > 0.05$ for both tests.)

Parity of mother—It might be expected that unsuccessful litters would occur more frequently among primiparae than among experienced mothers. There was no difference between the two groups, however ($\chi^2 = 0.486, df = 1, p > 0.1$).

LAP genotype—The LAP genotype (LeDuc and Krebs 1975) of the mother was not significantly associated with litter success ($\chi^2 = 1.544, df = 2, p > 0.1$).

Discussion

This study of *M. townsendii* provides new information concerning pre- and post-weanling survival of microtine rodents consistent with the existing evidence that survival up to the time of weaning is relatively high, while survival immediately after weaning is relatively poor. Many studies have reported very high loss rates of young microtines, but the trapping techniques used did not allow the loss to be separated into that occurring before weaning and that occurring after (Getz 1960; Golley 1961; Krebs *et al.* 1969). Where techniques were used that allowed the partitioning of the loss (Hoffman 1958; Boonstra and Krebs 1978), the estimates ranged from a 26% preweanling loss in *M. townsendii* to 38% loss in *M. montanus*. In the breeding enclosures 35% of litters were totally lost for reasons which cannot be attributed directly to trapping. These losses apparently occurred during the nestling stage, giving us an estimate of 65% nestling survival. This estimate must be considered a maximum, since the 25% loss in partially suc-

cessful litters also probably includes a preweanling component. In spite of the variety of methods employed in the studies cited here, they are all consistent with the hypothesis that survival of young voles for the nestling period is probably greater than 50%. Thus, if the very poor juvenile survival reported in peak and decline periods is not an artifact of trapping procedures (Chitty 1952; Chitty and Phipps 1966; Krebs *et al.* 1969; Boonstra 1976), it probably occurs primarily in the early postweanling stage.

The possibility that livetrapping studies are not sampling females randomly with respect to their ability to raise litters complicates the study of nestling and weanling survival, however. If those females most likely to lose their litters are never tallied as lactating because they avoid traps, then estimates of juvenile survival based on numbers of young voles trapped per lactating female may be too high. In addition, such a relationship between a female vole's trappability and her ability to bring her litter to weaning age suggests the possibility (further supported by behavioural studies reported in Anderson 1975) that mothers which are generally disposed to enter live traps regularly are somehow behaviourally well suited to nurturing their young, in spite of occasional nights away from them. Thus, a study of the behavioural relationship between mother and offspring should be an important part of any demographic study in which individual fitness and changes in population composition are investigated. Finally, of course, we must consider the further complication produced by the deleterious effects of trapping upon pregnancy and birth (see Table 7 and the "Effects of trapping" section). The mere fact that a population is exposed to periodic livetrapping may severely alter its reproductive characteristics, at least in *M. townsendii*.

The small enclosures at the Research Forest, by making possible the observation of individual reproductive performance, necessarily interfered with some aspects of the reproductive process as it would occur in an undisturbed population. Since this species is difficult to observe in nature, we assumed that individual adults would normally space themselves out and that a nursing female would attempt to discourage other adults, both male and female, from interfering with her litter. Rather than confine two adults in abnormally close quarters and risk this sort of interference, it seemed preferable to segregate extra adults from nursing females until the young left the nest (at which point they were removed from their enclosures, tagged, and released into a larger population). However, we have no way of knowing the extent to which

other adults influence the survival of nestlings in an undisturbed population. In a trapped population, females are separated from their litters for hours at a time, leaving them without maternal protection, which may result in increased interference by other adults. Until we can observe *M. townsendii* directly in natural habitat, this problem cannot be resolved satisfactorily.

The small enclosures may also have interfered with predation by weasels and snakes, but would not have discouraged a bear, raccoon, cat, or avian predator. In any trapping study, the voles are made more vulnerable than usual, during confinement, to bears, raccoons, and cats which learn how to open traps. On the other hand, traps probably protect them from avian predators. The major predators observed at Haney were hawks, owls, raccoons, and bears; the last two became quite efficient at opening traps. Weasels and snakes were seen only rarely. Thus, the enclosures probably produced the same biases in predation losses as any trapped area in similar habitat would.

The two aspects of reproduction most closely related to cyclic fluctuations in microtine populations, age at sexual maturity and length of breeding season (Krebs and Myers 1974), are best discussed in the context of a detailed population analysis. Here we note briefly that distribution of breeding effort throughout the year differed considerably between the two study areas. In the Research Forest population, reproduction typically continued at a low level throughout the winter and practically stopped during the summer in the small enclosures as well as on the larger adjacent grids. At Westham Island, the population bred throughout the summer and stopped in winter in both 1973 and 1974; but in 1975 when densities were extremely high, the breeding season was primarily confined to a spring period and a short fall period (Boonstra 1976). The midsummer lull in breeding had not previously been observed in that population. In addition, during 1975 at Westham Island, few young matured in the year of their birth. The age at sexual maturity appears, in part, to be related to the density of adult animals of the same sex (Boonstra 1976) and to be influenced by the environment shared by litter mates before weaning (Anderson 1975). Thus, the factors influencing these two important variables are complex and intimately tied to the state of the population.

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