Demography of *Microtus pennsylvanicus* in Southern Ontario: enumeration versus Jolly-Seber estimation compared

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A meadow vole population near Toronto went through a cycle in numbers from July 1978 to May 1982. The population never reached a density less than 96 voles/ha or greater than 630 voles/ha. Jolly-Seber estimates differed from total enumeration counts by an average of 10.6% in population size and by less than 0.03 per 2 weeks in survival rates for almost all periods. Sharp spring declines occurred in both sexes in both the increase and the peak years, but only among females in the decline year. Dispersal occurred more frequently during the spring of the increase and peak than of the decline, was associated with maturation, and was biased towards males. The breeding season lasted 9 months in the increase and decline but only 5 months in the peak. Survival of adults during the decline summer was no different from that in other years. Survival of young during the increase and peak was moderately high, but was extremely poor during the decline. Since most young failed to be captured in either pitfalls or live-traps, I conclude that they died shortly before or after weaning and suggest that maternal condition was impaired by prior events in the peak and that this may apply to other cyclic microtine populations.

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La densité d'une population de campagnols des champs près de Toronto a complété tout un cycle de juillet 1978 à mai 1982. Le nombre de campagnols dans la population n'a jamais diminué sous 96 individus/ha et n'a jamais dépassé 630 individus/ha. Les densités estimées selon la méthode Jolly-Seber diffèrent des densités déterminées par dénombrement total par 10,6% en moyenne, mais les taux de survie estimés selon cette méthode diffèrent par moins de 0,03 par 2 semaines à presque toutes les périodes. Il s'est produit des diminutions importantes des effectifs des deux sexes au printemps au cours de l'année d'augmentation et de l'année de densité maximale, mais cette diminution ne s'est manifestée que chez les femelles au cours de l'année de déclin de la population. La dispersion a été plus forte au cours des années d'augmentation et de densité maximale qu'au cours de l'année de déclin et ce phénomène est relié à la maturation et il est surtout l'apanage des mâles. La saison de reproduction a duré 9 mois au cours des années d'augmentation et de déclin, mais seulement 5 mois au cours de l'année de densité maximale. La survie des adultes au cours de l'été durant l'année de déclin ne différait pas de celle qui a été enregistrée les autres années. La survie des jeunes durant les années d'augmentation et de densité maximale s'est avérée modérément élevée, mais extrêmement faible durant l'année de déclin. Il y a eu peu de captures de jeunes dans les pièges à fosses et les pièges à bascule (animaux vivants) et il est probable que les jeunes sont morts peu avant le sevrage ou après; il se peut que la condition des mères ait été perturbée à certains moments au cours de l'année de densité maximale. Ces conclusions s'appliquent peut-être aussi à d'autres populations cycliques de microtinés.

[Traduit par le journal]

Introduction

Many populations of microtines, including the meadow vole, *Microtus pennsylvanicus*, do not cycle in the manner proposed by Krebs and Myers (1974). Since 1974, several long-term studies on the meadow vole have found only annual or occasionally cyclic fluctuations: Getz et al. (1979), Dueser et al. (1981), Baker and Brooks (1981), and Baird and Birney (1982). Only Tamarin (1977) found cycles in both populations that he examined. A syndrome of changes in birth and death rates characterizes cyclic populations. This paper documents a vole population in southern Ontario that shows most of these symptoms, but that in 5 years never fell below 96 voles/ha. This contrasts with the above recent studies in which the lowest densities reached were in the range of 0-40 voles/ha.

Total enumeration of population parameters has been used almost exclusively in long-term studies of small mammals, primarily because estimates may be biased by nonrandom sampling of marked and unmarked voles (Krebs 1966). Hilborn et al. (1976) have argued that under most conditions, the total enumeration method will underestimate a population by 10-20% when trappabilities are above 50%. Jolly and Dickson (1983) and Nichols and Pollock (1983) have argued that even under conditions of unequal catchability, the Jolly-Seber method is less biased than total enumeration. The second purpose of this paper is to compare these two methods of obtaining population statistics.

Methods

The study area and the trapping techniques have been described in Boonstra and Rodd (1983, 1984). The trapping grid was located at Pearson International Airport; it served as the control grid in the study of Boonstra and Rodd (1983) and was trapped from 26 June 1978 until 21 May 1982. The grid covered 0.7 ha of grassland with 100 trap points spaced 7.6 m apart. One of the two Longworth traps and one pitfall were placed at each trap point and were locked open when not in use. When first caught, voles were ear-tagged; tag number, location, weight, sex, and sexual condition were noted on each capture and then voles were immediately released. Live-traps and pitfalls were set for 2 days every 2nd week in summer; only live-traps were set in winter. Trappability estimates for this population are summarized in Krebs and Boonstra (1984) and were always above 50%.

Results

Population changes

I asked three questions about population changes: first, how did the Jolly-Seber estimator compare with total enumeration; second, did the population cycle; and third, were the changes similar between males and females? To allow comparison among years, I present data only for animals caught in live-traps, as pitfalls were not used every year.

Over the entire study the Jolly-Seber estimate was 10.6% (range 0-30%) higher than the total enumerated (Fig. 1). However, every year in the spring (March-April) and prior to the recruitment of the first young of the year, the two values

FIG. 1. Population changes in *Microtus pennsylvanicus* on a 0.7-ha trapping grid calculated by two methods: Jolly-Seber (Jolly); and minimum number known to be alive (MNA) of the total enumeration method. Nonbreeding periods are shaded.

were very similar, differing by no more than 5 animals in 1979, 1981, and 1982, and by 10 animals in 1980. The two values differed most markedly during the height of the breeding season and for up to 3 months after the end of it.

The population went through one cycle (Fig. 1). It was at peak densities when the study started in 1978. A sharp decline occurred in early 1979, followed immediately by an increase, which finally resulted in a peak in mid-1980. The subsequent, more gradual decline in 1980–1981 was not followed by an increase, but by a breeding season of no net growth, and a further decline in 1982. The 1979 decline differed from the 1980–1981 decline in that the former was associated with severe winter weather (Boonstra and Rodd 1983) whereas the latter was not.

The number of males and females generally fluctuated in a similar manner throughout most of the study, with female numbers often exceeding male numbers (Fig. 2). This was most pronounced in late 1980, when there were 30–60 more females in the trappable population. At the onset of the breeding season, males suffered sharper spring declines in the increase year (1979) and the peak year (1980) than did females, whereas in the decline year (1981), females sustained the most marked and prolonged decline. In 1982, neither sex showed a marked spring decline.

Reproduction

Changes in the length of the breeding season and in the intensity of breeding may be major forces in driving microtine cycles. The onset of the breeding season in any year was defined as the first trapping session in which >50% of the adult males were in breeding condition. The end of the breeding season was defined as the last trapping session in which <20% of the females were lactating. The breeding season lasted 9 months in the increase (1979) and decline (1981) years, but only 5 months in the peak year (1980) (see Fig. 1 for dates). The intensity of breeding, as measured by the percentage of adult females lactating in the period from May to mid-July (the height of the breeding season) was significantly less in 1981 (56%), than in 1979 (71%) or in 1980 (78%) ($\chi^2 = 51.1$, $df = 2$, $p < 0.001$). Virtually all adult males were in breeding

FIG. 2. Changes in the number of male and female *Microtus pennsylvanicus* calculated by the Jolly-Seber method. Nonbreeding periods are shaded.

condition at this time in each of these years. No females bred throughout the winter of any year, though a few lactating females were caught into January in both winters that followed summers of relatively low densities (winters of 1979–1980 and 1981–1982). Some males remained scrotal in all trapping sessions in the increase winter of 1979–1980 only.

Adult survival

The Jolly-Seber estimates of adult survival were compared with minimum survival rates (Krebs 1966). The mean Jolly-Seber estimates plus their standard errors were calculated according to the method of Carothers (1973). I recognized three periods in each biological year: the breeding season, the nonbreeding season, and the spring onset of the breeding season.

Four main points are shown by Fig. 3. First, the two estimators of survival were remarkably similar to each other over most of the study. In 10 of 12 average seasonal values in females and in 9 of 12 values in males, the two methods differed by no more than 0.03 per 2 weeks. However, the two estimates were more tightly correlated in males ($r = 0.81$, $N = 92$) than in females ($r = 0.62$). The Jolly-Seber estimates were clearly wrong a number of times, such as at the start of the sharp decline in the winter of 1978–1979, when the estimate was 1.19 in males and 1.32 in females. Overall, the Jolly-Seber estimate exceeded 1.00 eleven times in both males and females. Thus, at these times at least, the minimum survival rate gave a more biologically meaningful value than did the Jolly-Seber estimate. Second, adult males always survived more poorly during the breeding season than did females. However, in the nonbreeding season, adult males and females had virtually identical survival rates. Third, the survival of both sexes in the summer of 1981 was high and no different from that in other summers. Fourth, during all spring declines, males survived more poorly than did females, but this difference was greatest (0.22) in 1979 and 1980, and least (0.01–0.02) in 1981 and 1982.

Early juvenile survival

To obtain a measure of the production per pregnancy, I calculated an index of survival of the young. This index was the number of new young (<30 g) trapped per lactating female over the period of interest. Pitfalls are more likely than live-

FIG. 3. Survival of adult males and females calculated by the Jolly-Seber method (▲) and the total enumeration method (▽) (minimum survival rate). Period survival rates are also given for both estimates: Jolly-Seber (± 1 SE) (upper value) and minimum survival (lower value) for the summer breeding season (top two values), the winter nonbreeding season (middle two values), and the spring decline period (lower two values).

traps to capture young (Boonstra and Rodd 1984), but as I started using pitfalls only from the spring of 1979 onwards, I present one index for the animals entering live-traps only and another for the animals entering both trap types. Thus I could compare 1978 with other years. Three points can be made from Table 1. First, the production of young per pregnancy in 1978, when I did not trap in the spring, appears to have been similar to or perhaps slightly higher than it was in 1979 and 1980. Second, the number of lactating females seen over the entire season was reasonably similar in 1979, 1980, and 1981 (i.e., 490, 455, and 409 lactating females, respectively). Third, the total number of young produced was reasonably similar in 1979 and 1980 (456 and 546 young, respectively), but about twice as high as in 1981 (183 young). This resulted in an overall production of 0.93, 1.20, and 0.45 young per lactating female in 1979, 1980, and 1981, respectively. I conclude that the production of young in 1981 was greatly restricted.

Dispersal

I was able to capture a portion of the animals leaving the control grid and moving elsewhere, because other grids were being trapped in the area until the summer of 1981 (see Boonstra and Rodd (1983) and Rodd and Boonstra (1984) for

TABLE 1. Mean indices of early juvenile survival in *Microtus pennsylvanicus*

		Longworth live-trap juvenile population only	Longworth live-trap and pitfall juvenile populations combined
1978	5 July – 29 Sept.	0.74(182)	No pitfalls trapped
	11 Oct. – 22 Dec.	1.17(29)	No pitfalls trapped
1979	12 Apr. – 28 Sept.	0.55(316)	0.80(334)
	12 Oct. – 21 Dec.	0.74(155)	1.21(156)
1980	27 Mar. – 26 Sept.	0.59(455)	1.17(467)
1981	23 Apr. – 26 Sept.	0.32(326)	0.51(328)
	8 Oct. – 18 Dec.	0.19(81)	0.19(81)

NOTE: The index is the number of juvenile recruits (less than 30 g) per lactating female. Sample sizes of lactating females are in parentheses.

details of trapping dates of these other grids). Thereafter, only the control grid was trapped. When an animal moved from the control grid to another grid, it was assumed to have dispersed immediately after its last capture. In only three cases did a male move from the control grid to the adjacent grid and back again,

TABLE 2. Percent of *Microtus pennsylvanicus* from the control grid that were in breeding condition when arriving on another grid

	Males			Females				
	Adults and subadults		Juveniles	Adults and subadults		Juveniles		
	B	NB		B	NB	B	NB	
Spring reorganization								
1979 1 Mar. – 27 Apr.	80(5)	79(19)			50(4)			
1980 13 Mar. – 2 May	100(16)	91(35)			62(8)			
1981 26 Feb. – 7 May	100(5)	100(5)		100(4)	100(4)			
Main breeding season								
1979 10 May – 15 Aug.	92(13)	85(41)	61(23)	94(16)	80(10)	100(2)	57(7)	
1980 15 May – 15 Aug.	88(8)	20(15)	50(2)	100(3)	0(4)	0(1)	10(10)	
1981 19 May – 3 July	100(6)	100(3)	67(3)	100(5)	100(1)		80(5)	

NOTE: The breeding condition on last capture on the control grid is indicated by either B (in breeding condition before dispersing) or NB (not breeding before dispersing). The total number of animals dispersing is in parentheses. Animals caught in either trap type are included in the sample.

FIG. 4. Dispersal of *Microtus pennsylvanicus* from the grid to adjacent trapping areas. Nonbreeding periods are shaded.

and therefore the proximity of the adjacent grid is unlikely to have markedly affected the demography of the control. I recognize two periods of dispersal: the spring reorganization occurred just prior to or at the onset of breeding in the spring; and the main breeding season occurred as the majority of the young of the year started to enter the population.

Among males, the spring reorganization period was very different in 1981 from those in 1979 and 1980 (Fig. 4). Just prior to the onset of breeding in both 1979 and 1980, large numbers of males dispersed from the grid and were caught elsewhere. This did not happen in 1981. Of the males that disappeared, only 16% ($N = 49$) were caught elsewhere in 1981, compared with 62% ($N = 39$) in 1979 and 54% ($N = 95$) in 1980. Of the females that disappeared, less than 20% were caught elsewhere in any year (1979, 7% ($N = 21$); 1980, 17% ($N = 46$); 1981, 15% ($N = 46$)).

In both 1979 and 1980, the spring dispersal was followed by a month's lull in movements, and then another major bout of dispersal occurred in the main breeding season (Fig. 4). Of the males that disappeared, 87% ($N = 70$) were caught elsewhere in 1979, compared with 31% ($N = 61$) in 1980 and 21% ($N =$

TABLE 3. Median body weights at sexual maturity for *Microtus pennsylvanicus*, with 95% confidence limits in parentheses

	Males	Females
1978 Aug.	41(39–43)	44(41–47)
1979 May–July	30(29–32)	22(20–24)
1979 Aug.	35(33–37)	32(28–37)
1980 May – July 4	32(30–33)	29(27–32)
1980 July 14 – Aug.	42(39–44)	41(39–42)
1981 May–July	31(29–33)	28(25–31)
1981 Aug.	35(32–39)	28(24–33)

52) in 1981. Of the females that disappeared, 44% ($N = 63$) were caught elsewhere in 1979, compared with 14% ($N = 85$) in 1980, and 23% ($N = 43$) in 1981. Thus dispersal was a major factor accounting for disappearance during the increase year. The late breeding seasons and the nonbreeding seasons of 1978–1979, 1979–1980, and 1980–1981 were characterized by little or no dispersal.

Dispersal in small mammals is often associated with the onset of maturity. To examine this, I determined the breeding condition of all dispersers on last capture on the control grid and on first capture on another grid. Table 2 shows that during the spring reorganization, most dispersing nonbreeding adults and subadults on the control grid were captured elsewhere in breeding condition (88% of males and 69% of females pooled over all years). During the main breeding season, 1979 differed from 1980 in the percentage of nonbreeding adults, subadults, and juveniles captured elsewhere in breeding condition (for males, 77% in 1979 versus 23% in 1980 ($p < 0.001$); for females 71% in 1979 versus 7% in 1980 ($p < 0.001$)). In 1981, only a small number of animals dispersed, and virtually all nonbreeding dispersers from the control grid were captured elsewhere in breeding condition, as in 1979. I conclude that during the spring, most of the dispersal in males and females was associated with the transition from the nonbreeding to the breeding condition. This pattern was repeated in the main breeding season during the increase year (1979) but not during the peak year (1980). In addition to this, sizable numbers of animals dispersed when already in breeding condition (Table 2).

TABLE 4. Mean body weights ($\pm$ SE) of *Microtus pennsylvanicus* in the spring of each year

Males				Females			
Date	$\bar{x}$ weight	N	(%) >56 g	Date	$\bar{x}$ weight	N	(%) >44 g
1979 29 Mar.	46.1(0.77)	30	0	29 Mar.	38.7(0.76)	47	13
1980 10 Apr.	51.4(0.79)	64	22	27 Mar.	39.2(0.74)	96	24
1981 9 Apr.	45.4(0.71)	60	2	26 Mar.	34.0(0.46)	80	2
1982 22 Apr.	45.5(0.75)	30	0	8 Apr.	37.1(0.71)	42	2

NOTE: For males, the first trapping session in which >80% were scrotal was used. For females, the first trapping session that preceded by 4 weeks the trapping session in which >25% were lactating was used. 1980 was the peak year. Significant differences within a sex tested by ANOVA ($p < 0.05$) and are ranked as follows:

Males	1981	1982	1979	1980
Females	1981	1982	1979	1980

Sexual maturity

Differences in density and reproduction among years can be influenced by differences in age at sexual maturity. Since the age of the voles was unknown, I used weight as an index of age. The weight at sexual maturity for voles was calculated by the technique of Leslie et al. (1945). Maturity was judged in males by the presence of scrotal testes and in females by the presence of a perforate vagina, of lactation, or of pregnancy. All males matured at about the same weight in all spring – early summer periods, none matured in summers of high density (1978 and 1980), and some matured in summers of moderate density (1979 and 1981) but at about 4 g heavier than in the spring period (Table 3). Among females, maturation weight was 6 g lower in spring 1979 than in any other period. No females matured in summers of high density (1978 and 1980), and maturation weight was similar (28–32 g) in periods of moderate density.

Spring body weights

Peak populations of lemmings and voles typically contain adults much larger than those found in low or declining populations (Boonstra and Krebs 1979). I compared the spring body weights among years of males and females at the onset of breeding. I included females in this analysis by examining the trapping session 4 weeks before the 1st week in which >25% of the females were lactating. Thus, few females would have been pregnant at the time. In both sexes, animals from the peak year (1980) were heavier than those from other years (Table 4): in males, the peak animals were about 6 g heavier (13%); in females, peak animals were slightly heavier than increase animals (1979), but significantly heavier than the animals from the decline (1981) and from 1982. The lowest mean body weight among females occurred in 1981 when it was significantly less than in all other years.

Spring population dynamics

The spring decline is a characteristic feature of the population biology of all rodent populations (Krebs and Boonstra 1978). Its severity determines the breeding population for the summer. I looked for individual correlates of survival during the spring decline by comparing the following characteristics of voles that *did* and *did not* survive a 4-week interval at the onset of male reproduction each spring (Table 5): body weight at the start of the decline, week of first capture on the grid (index of age), number of wounds received during the interval, and breeding condition during the interval. The values of last two variables were determined by averaging the data for each individual over all his captures during the interval.

In all years, survivors in both sexes were more often in

breeding condition than nonsurvivors. Survivors were also heavier than nonsurvivors in both sexes; the difference was large in 1979 and 1980 (about 8 g in males and >10 g in females) but small in 1981 and 1982 (about 2–3 g in males and about 1 g in females). Among males, survivors were more heavily wounded than nonsurvivors; this difference was most pronounced in 1980 and 1981. Among females, survivors showed similar low wounding rates to nonsurvivors. Finally, only in 1979 were survivors younger than nonsurvivors, in both sexes. In all other years, survivors were generally older animals than non-survivors.

Discussion

The Jolly–Seber and the total enumeration techniques provided similar values for population size (Fig. 1) and survival (Fig. 3). Thus, if one can assume that the Jolly–Seber method generally provides estimates that are closer to true values (Jolly and Dickson 1983; Nichols and Pollock 1983), it is apparent that the total enumeration method is still a robust technique, a conclusion that Hilborn et al. (1976) reached. In addition, the Jolly–Seber estimates of survival are sometimes clearly wrong, such as when they exceed unity. Carothers (1973) found this occurring at low sampling intensities, a problem that seldom plagued my study. For those trapping periods when the Jolly–Seber estimates are clearly wrong, there is still room for minimum survival estimates to set a lower limit for survival. However, in general I would recommend using the Jolly–Seber method because it is usually less biased.

Most of the syndrome of changes in demography catalogued by Krebs and Myers (1974) occurred in this study. The population went through the multi-annual cycle, but the nature of the early 1979 decline differed fundamentally from the prolonged decline from fall 1980 to spring 1982 (an “H” decline in the terminology of Chitty (1955)). The 1979 nonbreeding decline coincided with freezing rain followed by cold temperatures (Boonstra and Rodd 1983). The 1980–1981 nonbreeding decline started in early fall, prior to any severe weather, and the winter was mild. Thus severe winter weather may be sufficient for a decline but not necessary (Fuller 1977). In addition, in the breeding season of 1979, a spring decline occurred with a great deal of male dispersal (Fig. 4), juvenile survival was good (Table 1), and the population grew rapidly (Fig. 1). None of these conditions were found in 1981. I suggest that the 1980–1982 decline is representative of a more “typical” cyclic decline (Krebs and Myers 1974), while the 1979 is not, and thus I will focus my attention on the 1980–1982 decline.

Typically, population declines in microtines result in very low numbers. However, the lowest density I recorded was

TABLE 5. Characteristics of voles that did and did not survive a 4-week period at the onset of breeding in spring

	Males		Females	
	Survivors	Nonsurvivors	Survivors	Nonsurvivors
Percent breeding (N)				
1979	57.7(26)	7.5(20)	5.8(43)	0(13)
1980	88.8(61)	64.0(50)	28.0(91)	0(15)
1981	86.0(50)	67.5(20)	9.7(74)	0(17)
1982	55.9(31)	14.3(14)	6.7(35)	0(11)
Body weight (SE)				
1979	49.7(1.44)	42.0(1.03)***	48.4(1.44)	33.6(1.08)***
1980	52.2(1.19)	43.6(1.07)***	46.4(0.91)	36.9(1.77)***
1981	42.9(1.08)	39.6(2.49)	34.0(0.68)	33.3(1.14)
1982	41.9(0.96)	39.8(1.21)	36.0(0.93)	34.8(1.80)
Number of wounds (SE)				
1979	0.34(0.13)	0.22(0.12)	0.05(0.02)	0
1980	2.32(0.27)	0.57(0.22)***	0.14(0.04)	0.07(0.07)
1981	1.55(0.22)	0.15(0.11)***	0.05(0.02)	0.12(0.12)
1982	1.30(0.27)	0.43(0.25)	0.19(0.06)	0.41(0.20)
Week of first capture (SE)				
1979	17.1(2.27)	9.4(2.03)**	14.6(1.71)	12.6(2.62)
1980	74.0(2.02)	79.1(1.60)	69.1(1.77)	71.5(3.28)
1981	115.8(2.37)	120.1(4.05)	114.0(1.54)	120.6(3.56)
1982	184.7(2.60)	189.6(3.70)	178.1(3.22)	191.8(2.90)*

NOTE: The start of the periods was as follows for each year: March 16, 1979, March 28, 1980, March 25, 1981, and March 25, 1982. The characteristics were percent breeding during the period, average body weight (grams) during the period, average number of wounds received during the period, and average week of first capture on grid. Samples sizes are presented in parentheses for the percent breeding only, but were the same in the other categories. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

96 voles/ha in 1979, 197 in 1981, and 114 in 1982. All were substantially above those reported in other studies of the meadow vole. Part of the explanation may be the absence of effective mammalian predators. Pearson (1971) postulated that low phases of cycles are maintained by predation. A weasel and weasel scats were seen only during a 2-week period in spring 1981, and short-tailed shrews, another possible predator, were absent altogether. Other ground and aerial predators were present at low levels throughout the study (R. Boonstra, personal observation). Typically, during breeding-season declines of microtines, both adult and juvenile survivals are low (Krebs and Myers 1974). However, in my study, while juvenile survival was very poor in 1981 (Table 1), adult survival was comparable to previous years (Fig. 3). Thus lack of effective mammalian predators may be involved in the high densities observed during population lows (cf. Krebs 1979).

A major difficulty in understanding the causes of juvenile mortality, especially during declines, is lack of good data on when it actually occurs. Does it occur prior to weaning or after it? Since pitfalls and live-traps failed to capture many young in 1981, whereas in other years and in one other area, both were effective in capturing young at an early age (Boonstra and Rodd 1984), yet large numbers of females were lactating, I conclude that juveniles were not leaving the nest and were dying near weaning. Godfrey (1955) reported similar findings in a decline year in *M. agrestis*. What are the possible causes for this? Severe nest predation is unlikely for the reasons given above. Infanticide by adult conspecifics is a possibility, although there is no good evidence that it is a significant cause of mortality in the field (Boonstra 1980). If it does occur, it is more likely to

be perpetrated by adult females than by males (Boonstra 1984; Brooks 1984). However, I believe the evidence suggests that the cause is related to some aspect of maternal condition, which resulted in an inability of the females to properly nurture their young. In 1981, resident females had the lowest spring body weights of any year (Table 4) and the lowest intensity of breeding during the period of maximum reproduction (May–mid-July). The energetic costs of lactation are high in small mammals (Migula 1966; Millar 1979). Chitty (1952) proposed that females born during peak years were physiologically deranged as a result of intraspecific strife amongst their parents and that these females transmitted the defects to their offspring in the decline. Though such ideas were later largely abandoned by Chitty (1967), I believe they still have merit. The hormonal environment of the fetus can impair subsequent adult behavior and fertility (Christian and LeMunyan 1957; Herrenkohl 1979; Ward and Weisz 1980; Pollard 1984). Thus, to understand breeding season declines in microtines, I would strongly recommend investigating this area further by using the techniques of Bradley et al. (1980) and McDonald and Taitt (1982).

Finally, how important is synchrony in the onset of breeding in large numbers of animals to the production of peak populations? Boonstra and Rodd (1983) found that in *M. pennsylvanicus*, more breeding males could occupy an area if they all came into breeding condition at once than if a much smaller number came into breeding condition at the start of the breeding season. In the latter case, even though large numbers of breeding males were being produced in the population, few were recruited (Tables 2 and 3) because they were apparently prevented from doing so by the breeding males already there.

Taitt and Krebs (1983) extended this idea by suggesting that synchrony in onset of breeding in both sexes in large spring populations sets the stage for peak populations. It is clear from my data that synchrony in onset of breeding among females is not essential to the production of a large breeding population of females (e.g., 1979), though the large numbers of females present in the spring of the peak year (1980) may have facilitated the production of a peak (see also Redhead (1982) for similar conditions resulting in the outbreak of a house mouse population in Australia). In addition, conditions, as during the decline year, may be such that the presence of large numbers of breeding females is not sufficient for the production of a peak population. Large numbers of breeding females were present in the spring of 1981 (Fig. 2), yet the population did not grow at all, whereas it had grown rapidly in 1980 under similar conditions. Thus, some other qualitative difference in either the animals (such as that suggested above) or the environment must explain why the population grew in one year and not in the next.

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- BAIRD, D. D., and E. C. BIRNEY. 1982. Characteristics of dispersing meadow voles *Microtus pennsylvanicus*. *Am. Midl. Nat.* **107**: 262–283.
- BAKER, J. J., and R. J. BROOKS. 1981. Distribution patterns of raptors in relation to density of meadow voles. *Condor*, **83**: 42–47.
- BOONSTRA, R. 1980. Infanticide in microtines: importance in natural populations. *Oecologia*, **46**: 262–265.
- . 1984. Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) toward young. *Oecologia*, **62**: 126–131.
- BOONSTRA, R., and C. J. KREBS. 1979. Viability of large- and small-sized adults in fluctuating vole populations. *Ecology*, **60**: 567–573.
- BOONSTRA, R., and F. H. RODD. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *J. Anim. Ecol.* **62**: 757–780.
- . 1984. Efficiency of pitfalls versus live-traps in enumeration of populations of *Microtus pennsylvanicus*. *Can. J. Zool.* **62**: 758–765.
- BRADLEY, A. J., I. R. McDONALD, and A. K. LEE. 1980. Stress and mortality in a small marsupial (*Antechinus stuartii* Macleay). *Gen. Comp. Endocrinol.* **40**: 188–200.
- BROOKS, R. J. 1984. Causes and consequences of infanticide in populations of rodents. In *Infanticide in animals and man*. Edited by G. Hausfater and S. B. Hrdy. Aldine Press, Chicago. pp. 331–348.
- CAROTHERS, A. D. 1973. Capture-recapture methods applied to a population with known parameters. *J. Anim. Ecol.* **42**: 125–146.
- CHITTY, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–9. *Philos. Trans. R. Soc. London, Ser. B*, **236**: 505–552.
- . 1955. Adverse effects of population density upon viability of later generations. In *The numbers of man and animals*. Edited by J. B. Cragg and N. W. Pirie. Oliver and Boyd, Ltd., Edinburgh. pp. 57–67.
- . 1967. The natural selection of self-regulatory behaviour in animal populations. *Proc. Ecol. Soc. Aust.* **2**: 51–78.
- CHRISTIAN, J. J., and C. D. LEMUNYAN. 1957. Adverse effects of crowding on reproduction and lactation of mice and two generations of their progeny. *Nav. Med. Res. Inst., Res. Rep. NM 24 01.04.01*, **15**: 925–936.
- DUESER, R. D., M. L. WILSON, and R. K. ROSE. 1981. Attributes of dispersing meadow voles in open-grid populations. *Acta Theriol.* **26**: 139–162.
- FULLER, W. A. 1977. Demography of a subarctic population of *Clethrionomys gapperi*: numbers and survival. *Can. J. Zool.* **55**: 42–51.
- GETZ, L. L., F. R. COLE, L. VERNER, J. E. HOFMANN, and D. AVALOS. 1979. Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus*. *Acta Theriol.* **24**: 319–349.
- GODFREY, G. K. 1955. Observations on the nature of the decline in numbers of two *Microtus* populations. *J. Mammal.* **36**: 209–214.
- HERRENKOHL, L. R. 1979. Prenatal stress reduces fertility and fecundity in female offspring. *Science (Washington, D.C.)*, **206**: 1097–1099.
- HILBORN, R., J. A. REDFIELD, and C. J. KREBS. 1976. On the reliability of enumeration for mark and recapture census of voles. *Can. J. Zool.* **54**: 1019–1024.
- JOLLY, G. M., and J. M. DICKSON. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. *Can. J. Zool.* **61**: 922–927.
- KREBS, C. J. 1977. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecol. Monogr.* **36**: 239–273.
- . 1979. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. *Fortschr. Zool.* **25**: 61–77.
- KREBS, C. J., and R. BOONSTRA. 1978. Demography of the spring decline in populations of the vole, *Microtus townsendii*. *J. Anim. Ecol.* **47**: 1007–1015.
- . 1984. Trappability estimates for mark-recapture data. *Can. J. Zool.* **62**: 2440–2444.
- KREBS, C. J., and J. H. MYERS. 1974. Population cycles in small mammals. *Adv. Ecol. Res.* **8**: 267–399.
- LESLIE, P. H., J. S. PERRY, and J. S. WATSON. 1945. The determination of the median body-weight at which female rats reach maturity. *Proc. Zool. Soc. London*, **115**: 473–488.
- McDONALD, I. R., and M. J. TAITT. 1982. Steroid hormones in the blood plasma of Townsend's vole (*Microtus townsendii*). *Can. J. Zool.* **60**: 2264–2269.
- MIGULA, P. 1969. Bioenergetics of pregnancy and lactation in the European common vole. *Acta Theriol.* **14**: 167–179.
- MILLAR, J. S. 1979. Energetics of lactation in *Peromyscus maniculatus*. *Can. J. Zool.* **57**: 1015–1019.
- NICHOLS, J. D., and K. H. POLLOCK. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. *J. Mammal.* **64**: 253–260.
- PEARSON, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *J. Mammal.* **52**: 41–49.
- POLLARD, I. 1984. Effects of stress administered during pregnancy on reproductive capacity and subsequent development of the offspring of rats: prolonged effects on the litters of a second pregnancy. *J. Endocrinol.* **100**: 301–306.
- REDHEAD, T. D. 1982. Reproduction, growth and population dynamics of house mice in irrigated and non-irrigated cereal farms in New South Wales. Ph.D. thesis, Australian National University, Canberra.
- RODD, F. H., and R. BOONSTRA. 1984. The spring decline in the meadow vole, *Microtus pennsylvanicus*: the effect of density. *Can. J. Zool.* **62**: 1464–1473.
- TAITT, M. J., and C. J. KREBS. 1983. Predation, cover, and food manipulation during a spring decline of *Microtus townsendii*. *J. Anim. Ecol.* **52**: 837–848.
- TAMARIN, R. H. 1977. Demography of the beach vole (*Microtus breweri*) and the meadow vole (*M. pennsylvanicus*) in southeastern Massachusetts. *Ecology*, **58**: 1310–1321.
- WARD, I. L., and J. WEISZ. 1980. Maternal stress alters plasma testosterone in fetal males. *Science (Washington, D.C.)*, **207**: 328–329.