

Life on the edge: the demography of short-season populations of deer mice

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We documented populations of deer mice in the Kananaskis Valley, southwestern Alberta, Canada from 1979 to 1997 to determine whether these short-season populations were more, or less, variable than populations in more temperate environments. We then examined patterns of reproduction, age-specific survival, and immigration to explain variation in summer population growth. Population densities showed no multi-annual periodicity and were generally low. At maximum, numbers doubled over the breeding season, but declined over the breeding season in 4 of 16 yr. Variability in population density was low, and similar to that of *Peromyscus* populations in more temperate environments. No demographic parameters were related to spring population densities, and immigration rates were low when conditions for survival of nestlings and adults were favorable. Variation in summer population growth was attributed primarily to variation in nestling survival among years.

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Reproduction in some northern and alpine small mammals is constrained such that maturation occurs much later than in temperate environments. For example, deer mice, *Peromyscus maniculatus*, mature at one year of age in northern environments rather than during the summer of their birth as in temperate environments (Gilbert and Krebs 1981, 1991, Gyug and Millar 1981, Van Horne 1981, Millar 1982, 1994, Millar and Innes 1985, Lusk and Millar 1989, Teferi and Millar 1993). The same pattern of delayed maturation has been recorded in a number of northern and alpine microtine rodents, including common voles, *Microtus arvalis*, and snow voles, *Chionomys nivalis* (Yoccoz and Ims 1999), root voles, *M. oeconomus* (Kostian 1970), longtail voles, *M. longicaudus* (Van Horne 1982), and taiga voles, *M. xanthognathus* (Wolff and Lidicker 1980). Similarly, species that normally mature as yearlings may not mature until two years of age in northern and alpine environments (see Sheppard 1969, Zammuto and

Millar 1985, Dobson and Murie 1987, Falk and Millar 1987, Becker et al. 1998).

Populations in which maturation is delayed can only be sustained if there is compensatory reproduction during a short breeding season, or if survival and longevity are enhanced relative to populations with earlier maturation. Available evidence indicates that enhanced survival and longevity provides the primary compensation for delayed maturation in northern and alpine environments (Millar 1984, 1994, Zammuto and Millar 1985, Dobson and Murie 1987, Yoccoz and Mesnager 1998). Populations with delayed maturation have a longer generation time and a slower turn-over time than those with early maturation.

The population consequences of a slow turn-over time are not clear. Intuitively, one might expect such populations to exhibit less variation than those with a rapid turn-over because they have a low potential for population growth (e.g. Yoccoz and Ims 1999). Alter-

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natively, slow turn-over systems in northern environments are vulnerable to perturbation (Dunbar 1973) and some northern populations of small mammals are noted for their large fluctuations in density (Hansson and Henttonen 1985, 1988, Ostfeld 1988, Krebs 1996). Yoccoz and Ims (1999) found populations of alpine snow voles and common voles (with delayed maturation) to exhibit low population variability relative to arctic sibling voles, *M. rossiaemeridionalis* (with early maturation). A lack of studies in alpine environments precludes generalized conclusions (Yoccoz and Ims 1999).

The life history patterns of deer mice in the Kananaskis Valley, southwestern Alberta, Canada clearly exhibit the characteristics of a slow turn-over population. Breeding by young-of-the-year is rare in these populations (Teferi and Millar 1993, McAdam and Millar 1999) and survival and longevity are enhanced relative to populations in more temperate environments (Millar 1994). However, it is not known whether these slow turn-over characteristic result in more or less variable populations than *Peromyscus* in other environments.

Population and demographic data for sub-alpine populations of deer mice were recorded in the Kananaskis Valley during most years from 1979 to 1997. Here we record their multi-annual population variability and examine the relationship between demography and summer population growth in these mice.

Methods

Individual mice were monitored by live-trapping from early May through late August during most years from 1979 to 1997. At first capture, each mouse was ear-tagged, weighed (nearest 0.5 g on a Pesola spring scale), sexed, and aged based on pelage characteristics (brown pelage = overwintered; grey pelage = young-of-the-year). During each subsequent capture, data were collected on weight and reproductive condition. Females were recorded as pregnant (swollen abdomen), lactating (visible nipples), both pregnant and lactating or non-breeding, and males were recorded as testes scrotal or testes abdominal. For breeding females, the mid-date between last capture as pregnant and first capture as lactating was recorded as the parturition date. Because average litter size is 5.25 (Millar and Innes 1983), number of parturitions \times 5.25 provided an estimate of total young born on each grid each year.

Number of young weaned on each grid was determined in two ways. Before 1985, weaned young were distinguished from immigrants based on weight at first capture. Powder-tracking to locate nest sites (Lemen and Freeman 1985) was initiated in 1985 (Sharpe and Millar 1990) and additional traps were set near the nest site to capture weaned young in subsequent years. This

change in protocol may have had some effect on counts of number of young weaned before and after 1985, although the bias was likely not great because young-of-the-year deer mice in the Kananaskis Valley are highly philopatric (Teferi and Millar 1994).

Other trapping protocols also varied somewhat from year to year. For example, trapping frequency ranged from one night twice-weekly to one night each week, trapping grids varied in size (range 1.3–6.0 ha), the number of years individual grids were monitored varied (range 1–11 yr), number of grids monitored each year varied (range 0–6), and grid locations ranged throughout the Kananaskis Valley, from Barrier Lake to the boundary of Peter Lougheed Park (a distance of 35 km). In addition, information for some grids was available only from published sources (e.g. Millar and Innes 1983, Lusk and Millar 1989) while raw data (unpubl.) were available for others. For these reasons, the data considered here were restricted to parameters that could be obtained from both published and unpublished sources.

Spring densities were recorded as the number of overwintered males and females resident for at least 14 d in early May and fall densities were recorded as the total number of mice (including immigrant) resident for at least 14 d in late August. Grids that were used for removal experiments (e.g. see Teferi and Millar 1993), and other experimental manipulations that influenced population growth (e.g. see McAdam and Millar 1999) were excluded. However, experimental grids that have no effect on reproduction or survival (e.g. see Woolfenden and Millar 1997) were included.

Number of young born on each grid could be recorded because individual mice were monitored consistently in all years. Survival, per se, over the breeding season could not be determined because we had no measure of emigration, but could be estimated because overwintered adults and YY were tagged, and their presence or absence was known in the fall. Instantaneous rates of change per week provided indices of survival, calculated over 17 weeks (pre-breeding to fall) for adults, three weeks (birth to weaning) for nestlings, and eight weeks (weaning to fall) for independent YY. All mice present in the fall that were not tagged in the spring or at weaning were considered to be immigrants. Because virtually all immigrants were YY, rates of immigration could be quantified relative to weaned young as instantaneous rates calculated over eight weeks. This index provided a relative measure of immigration relative to the number of weaned young whereby an index > 0 indicated more immigrants than weaned young, and an index < 0 indicated fewer immigrants than weaned young. Population growth over the summer was calculated as

$$r = \frac{\ln N_{\text{fall}} - \ln OW_{\text{spring}}}{17} \quad (1)$$

where r = the intrinsic rate of increase week⁻¹, N_{fall} = total mice in the fall, OW_{spring} = number of overwintered mice in the spring, and 17 = the number of weeks between spring and fall. Finally, population variability among years was calculated for spring and fall densities as the standard deviation of log density following Hansson and Henttonen (1985). This measure was used in order to be consistent with previous studies of population variability in small mammals. However, recognizing that this measure is potentially subject to bias due to differences in mean density (McArdle et al. 1990, McArdle and Gaston 1995, Stewart-Oaten et al. 1995) we also provide coefficients of variation for our data. Summer population growth rates were tested for autocorrelation among years following Legendre and Legendre (1998).

Results

Data were available for 17 of the 19 yr from 1979 to 1997. However, in one year (1984) trapping was not initiated until June so that no data were available for early May. Therefore, spring densities (early May), patterns of reproduction and survival, and summer population growth were known for 16 yr, while peak population densities (late August) were known for 17 yr.

Population density

Estimates of population density may have been biased among years because grid sizes varied. For this reason, we first examined the effects of grid area on population

density. The average spring density per grid ($N = 12$ grids) was negatively related to grid size as

$$D_{\text{spring}} = 12.25 - 1.55 \text{ Area} \quad (2)$$

where D_{spring} = density in May and Area = grid size in hectares ($r = -0.62$, $N = 12$, $P = 0.03$). Therefore, the density for each grid in May each year was corrected to the average grid size (2.35 ha).

The average fall density per grid ($N = 13$ grids) was not significantly related to grid size ($r = -0.35$, $N = 13$, $P = 0.26$), but a negative trend similar to that for spring densities was also evident as

$$D_{\text{fall}} = 12.49 - 1.02 \text{ Area} \quad (3)$$

where D_{fall} = density in August and Area = grid size in hectares. For this reason, the density for each grid in August each year was also corrected to the average grid size (2.35 ha).

A summary of average population densities and population growth over the summer (Table 1) indicates that densities in early May ranged from 5.0 to 15.4 ha⁻¹, while fall densities ranged from 1.0 to 17.6 ha⁻¹. Population variability appeared to be greater at the end of the breeding season than during the pre-breeding season ($s = 0.303$ vs 0.155 and $CV = 0.443$ vs 0.367, respectively). To test the critical assumption that variability was unrelated to density, we regressed log s and log CV against log density during spring and fall, using all grids monitored in more than one year ($N = 9$ grids). Because one grid had the same fall density in the only two years it was trapped, a small constant (0.0001) was added to both log s and log density in the fall. Both s and CV were negatively related to density in the spring

Table 1. Population densities, population variability and summer population growth of deer mice in the Kananaskis Valley, Alberta from 1979 to 1997. All densities ($N/\text{ha} \pm 1 \text{ SE}$) were corrected to an average grid size of 2.35 ha, and population growth (r) was based on the difference in mean corrected density over 17 weeks, from spring (early May) to fall (late August).

Year	N grids	Early May density	Late August density	Population growth
1979	1	6.6	9.4	0.021
1980	2	7.1 \pm 3.3	8.8 \pm 0.9	0.012
1981	2	6.8 \pm 1.3	2.2 \pm 1.0	-0.067
1984	1	-	7.9	-
1985	3	9.1 \pm 0.2	10.9 \pm 1.3	0.011
1986	2	13.9 \pm 1.4	17.6 \pm 1.0	0.014
1987	4	15.4 \pm 4.4	9.4 \pm 1.6	-0.029
1988	4	9.1 \pm 2.3	13.0 \pm 1.6	0.021
1989	5	10.2 \pm 1.4	14.4 \pm 2.5	0.020
1990	5	10.2 \pm 1.7	12.4 \pm 2.0	0.011
1991	5	11.3 \pm 1.4	11.3 \pm 2.5	0.000
1992	4	10.6 \pm 0.9	5.8 \pm 2.9	-0.035
1993	4	5.0 \pm 3.2	1.0 \pm 0.7	-0.093
1994	6	5.4 \pm 2.4	10.0 \pm 4.7	0.036
1995	6	5.3 \pm 1.4	6.2 \pm 1.1	0.010
1996	5	5.3 \pm 1.7	9.1 \pm 3.0	0.032
1997	4	6.7 \pm 1.9	8.0 \pm 22.2	0.011
		$s = 0.155$	$s = 0.303$	
		$CV = 0.367$	$CV = 0.443$	

Table 2. Number of overwintered mice, number of parturitions, number of mice born, weaned and resident in late August, number of young-of-the-year breeding, and number of immigrant deer mice recorded in the Kananaskis Valley from 1979 to 1997. Values are summed over all grids for each year. Number of mice born was estimated as number of parturitions \times 5.25. Number of adults and young-of-the-year remaining in late August from 1979 to 1981 were extrapolated using survival estimates in Millar and Innes (1983). Survival estimates in Lusk and Millar (1989) were used to derive similar estimates for one of three grids recorded in 1985.

Year	Overwintered adults			Young-of-the-year					Immigrants		Total
	resident in early May (A)	remaining in late August (B)	no. of parturitions (C)	no. born (D)	no. weaned (E)	remaining in late August (F)	no. of parturitions (G)	resident in late August (H)	resident in late August (I)		
1979	16	6	25	131	47	14	0	11	31		
1980	27	2	19	99	36	13	0	30	45		
1981	34	4	27	142	6	0	0	5	9		
1985	72	12	56	294	157	96	8	20	128		
1986	101	31	88	462	206	104	6	18	153		
1987	105	31	49	256	49	27	0	10	68		
1988	67	21	36	189	67	40	0	32	93		
1989	106	28	59	309	109	83	2	36	147		
1990	109	29	55	288	108	80	1	22	131		
1991	113	28	50	263	126	81	4	16	125		
1992	78	11	53	277	58	22	0	14	47		
1993	36	2	10	52	14	4	0	5	11		
1994	55	25	34	181	110	69	5	6	100		
1995	64	14	41	216	80	35	2	33	82		
1996	56	9	48	252	120	56	5	26	91		
1997	49	12	41	216	74	40	0	4	56		

Table 3. Proportional demographic responses of deer mice in the Kananaskis Valley among years, derived from Table 2. Survival rates are instantaneous rates per week, calculated over 17 weeks (pre-breeding to fall) for adults, three weeks (birth to weaning) for nestlings, and eight weeks (weaning to fall) for independent young-of-the-year. Immigration rates were calculated relative to the number of weaned young, over eight weeks. Because no weaned young survived the summer of 1981, a constant (1) was added to the number of weaned and remaining in late August, in order to calculate YY survival in that year.

Year	Overwintered adults			Young-of-the-year			Immigrants relative to weaned young (E vs H)
	summer survival (A vs B)	per capita parturition (C/A)	nestling survival (D vs E)	summer survival (E vs F)	per capita parturitions (G/E)		
1979	-0.058	1.560	-0.342	-0.151	0.000	-0.182	
1980	-0.015	0.700	-0.337	-0.127	0.000	-0.023	
1981	-0.013	0.790	-1.055	-0.106	0.000	-0.023	
1985	-0.105	0.780	-0.209	-0.061	0.050	-0.258	
1986	-0.069	0.870	-0.269	-0.085	0.030	-0.305	
1987	-0.072	0.470	-0.551	-0.074	0.000	-0.199	
1988	-0.068	0.540	-0.346	-0.064	0.000	-0.092	
1989	-0.078	0.560	-0.347	-0.034	0.020	-0.138	
1990	-0.078	0.500	-0.327	-0.038	0.010	-0.199	
1991	-0.082	0.440	-0.245	-0.055	0.030	-0.258	
1992	-0.115	0.680	-0.521	-0.121	0.000	-0.178	
1993	-0.170	0.280	-0.437	-0.157	0.000	-0.129	
1994	-0.046	0.610	-0.106	-0.058	0.050	-0.364	
1995	-0.089	0.640	-0.331	-0.103	0.020	-0.111	
1996	-0.108	0.860	-0.247	-0.095	0.040	-0.191	
1997	-0.083	0.840	-0.357	-0.077	0.000	-0.385	

($r^2 = 0.71$, $P = 0.004$ and $r^2 = 0.62$, $P = 0.011$, respectively) and in the fall ($r^2 = 0.043$, $P = 0.055$ and $r^2 = 0.66$, $P = 0.015$, respectively). From this, our measures of population variability were biased towards greater variability at low densities than high densities, and our finding of greater variability in the fall than spring is real.

Population growth during the summer was negative in 4 of 16 yr (1981, 1987, 1992, 1993). Population changes over winter could not be consistently assessed from these data because grids monitored in the spring were not necessarily those monitored the previous fall. However, increases in density over some winters (1984–1985, 1985–1986, 1993–1994) indicates that immigration contributed significantly to spring density on trapping grids in some years.

Demography

Patterns of reproduction, nestling survival, survival of overwintered adults and YY, and immigration were summed over all grids within each year (Table 2). Because the number and size of grids monitored varied annually, the number of overwintered adults, parturitions and young born, and mice in the fall were influenced by the intensity of sampling each year. Therefore, instantaneous rates of change were used to compare differences in demographic variables among years (Table 3). Variation in some demographic variables among years was considerable. For example, rates of decline of adults throughout the breeding season ranged from -0.170 (in 1993) to -0.046 (in 1994), the rates of decline between birth and weaning ranged from -1.055 (in 1981) to -0.166 (in 1994), rates of decline of weaned YY throughout the breeding season ranged from -0.157 (in 1993) to -0.034 (in 1989), and rates of immigration ratio ranged from -0.364 (in 1994) to -0.023 (in 1980/81). However, the per capita parturition rate did not show extreme variation (except in 1979 when the single population monitored showed a skewed sex ratio of 11 females, 5 males). The number of breeding YY females was zero or relatively low in all years. None of the demographic parameters exhibited a multi-annual periodicity (Table 2) and none were significantly related to spring population density ($r^2 < 0.15$, $P > 0.05$).

Explaining summer population growth

Autocorrelation coefficient ranged from -0.07 to -0.43 (95% confidence limits = ± 0.72), indicating that summer population growth was independent for time lags of 1–4 yr. Summer population growth was also unrelated to spring population density ($r^2 = 0.00003$, $P = 0.98$, $N = 16$), so variation in population growth must be attributed to demographic events during the

Table 4. Correlation coefficients among summer population growth (Table 1) and demographic variables (Table 3) for deer mice over 16 yr. * denotes $P < 0.05$; ** denotes $P < 0.01$.

	Adult survival	Adult parturitions	Nest survival	Young survival	Immigration rate
Summer growth	0.66*	0.36	0.71**	0.48	-0.38
Adult survival		0.28	-0.36	0.58*	-0.56
Adult parturitions			0.02	-0.36	-0.10
Nest survival				0.29	-0.54*
YY survival					-0.39

breeding season. To determine which demographic parameters explain variation in population growth, we first assessed population growth in relation to each demographic variable, and the interrelationship among the demographic variables (Table 4). Immigration rates were inversely related to adult survival and nestling survival. As such, immigrants tended to compensate for mortality of adults and nestling, but did not explain a significant amount of the variation in summer population growth table (Table 4). The survival of adults and independent young were also related but nestling survival was independent of both adult and YY survival. Summer population growth was positively related to both nestling and adult survival, but not related to any other demographic variable. Multiple step-wise regression of summer population growth on both nestling and adult survival indicated that these two variables account for most of the variation in summer population growth ($R^2 = 0.69$, $P = 0.014$), with most of the variation explained by nestling survival ($R^2 = 0.51$, $P = 0.002$).

Discussion

Populations of deer mice in the Kananaskis Valley are characterized by low population densities (approximately five per hectare) in spring, and moderate population growth (approximately a doubling of density) over the breeding season. This moderate population growth is attributable to the fact that multiple generations per breeding season are rarely possible, due to time and nutritional constraints on growth and maturation of young-of-the-year mice (McAdam and Millar 1999). Multi-annual changes in population density show no clear pattern of periodicity, and relatively low population variability ($s = 0.155$ in early May and 0.303 in late August). Yoccoz and Ims (1999) found low population variability in alpine snow voles and common voles that matured as yearlings, relative to northern sibling voles that matured early in life. The pattern of population variability observed in this study appears to be more similar to that of snow and common voles than sibling voles. However, the low population variability in subalpine deer mice does not appear to be a direct result of low population turnover. Low population variability appears to be a characteristic of all

Peromyscus populations, irrespective of differences in the duration of the breeding season and the potential for multiple generations per breeding season. Population variability has been recorded over six or more years for 11 populations of *Peromyscus* (Table 5), but no geographical trend in variability is evident. Nor is there any consistent pattern of variability between the beginning and end of the breeding season among the northern populations. Two populations tended to be more variable in May than August (Mackenzie and Kluane) while two tended to be more variable in August than May (Heart Lake and Kananaskis). These estimates may suffer from biases related to differences in mean density (McArdle et al. 1990, McArdle and Gaston 1995, Stewart-Oaten et al. 1995), as ours do, but, based on available data, there is no obvious pattern of greater or lesser variability in northern vs southern populations of mice.

The greater variability of fall populations relative to spring populations of subalpine deer mice ($s = 0.30$ vs 0.15) is clearly related to variation in population growth over the breeding season. Summer population growth ranged from -0.093 to 0.036 , with negative growth recorded in 4 of 16 yr. Such declines over the breeding season are not uncommon in populations of small mammals. For example, Gilbert and Krebs (1991) noted similar declines in northern populations of deer mice (three consecutive seasons in 13 yr) and northern red-backed voles, *Clethrionomys rutilus* (once in 13 yr). Numerous short-term studies have also recorded summer declines (e.g. Elton et al. 1935, Godfrey 1955, Henttonen et al. 1987, Chitty 1996) that were generally attributed to "failure of recruitment". In the present study, variability in summer population growth was clearly related to mortality rather than reproductive potential, with nestling survival being the single most important contributor to this variation. Survival of overwintered mice also contributed to variation in population growth over the summer but to a lesser extent than nestling survival.

It is of interest to note that neither summer population growth nor any of the demographic variables were related to spring population density. This indicated that spring population levels are likely governed by limited resources during the winter, rather than during the summer, and that constraints on reproduction preclude the attainment of numbers sufficient to invoke density

Table 5. Population variability, measured as the standard deviation of log density, among populations of *Peromyscus*. Mice at Heart Lake, Mackenzie, Kluane, and Kananaskis are known to delay maturation to one year of age, while the remaining populations are in more temperate environments where multiple generations are possible during the breeding season.

Species	Location	N years	Annual sample	Population variability	Source
<i>P. maniculatus</i>	Heart Lake, NWT	10	May	0.20	Fuller 1985
			August	0.26	
<i>P. maniculatus</i>	Mackenzie, NWT	10	May	0.21	Fuller 1985
			August	0.19	
<i>P. maniculatus</i>	Kluane, Yukon	14	May	0.26	Gilbert and Krebs 1991
		13	August	0.21	
<i>P. maniculatus</i>	Kananaskis, Alberta	16	early May	0.15	Present study
		17	late August	0.30	
<i>P. maniculatus</i>	Algonquin, Ontario	43	summer and fall	0.20	Fryxell et al. 1998
<i>P. maniculatus</i>	Mountain Lake, VA	6	peak summer	0.18	Krohne et al. 1988
<i>P. maniculatus</i>	Powdermill, PA	7	peak summer	0.30	Krohne et al. 1988
<i>P. leucopus</i>	Allee Wood, IN	6	peak summer	0.22	Krohne et al. 1988
<i>P. leucopus</i>	Mountain Lake, VA	6	peak summer	0.37	Krohne et al. 1988
<i>P. leucopus</i>	Powdermill, PA	7	peak summer	0.25	Krohne et al. 1988
<i>P. leucopus</i>	Carter Woods, OH	6	peak summer	0.37	Krohne et al. 1988

effects. The causes of nest mortality are difficult to determine directly because subalpine deer mice nests are underground and females relocate nests frequently (Sharpe and Millar 1990), but it is apparent that the factors causing death in the nest are specific to nestlings and do not have major impact on older age groups. This is evident from the fact that nestling survival is not significantly related to adult or YY survival (Table 4) and the fact that not all years with high nestling mortality had high adult mortality (Table 3). In some populations of small mammals, heavy nest mortality has been attributed to predation by snakes (e.g. Getz et al. 1990), and mortality by snakes might be nestling-specific. However, no snakes have been recorded on any of our subalpine study sites. Predation by mustelids might also be expected to have the potential to influence nest mortality, but small mustelids (*Mustela erminea*) were not commonly recorded on our study sites. Summer food resources also appear not to influence nestling survival because the addition of food, which had a positive effect on growth of nestlings and rates of maturation, had no effect on the success rate of litters in the nest (McAdam and Millar 1999). Finally, social factors, such as infanticide (Wolff and Peterson 1998), or diseases might influence nest mortality, but such effects should be expected to operate in a density dependent fashion, which is not the case here. This leaves meteorological conditions as the most likely explanation for nest mortality. We already know that the differential mortality of young males and females in the nest is related to weather (Havelka and Millar 1997), and general levels of nest mortality might be influenced by weather as well. Whatever the cause of nest mortality its importance to dynamics of subalpine deer mouse populations is clear. Without nest mortality, breeding is sufficient (two litters of five young per season) to increase populations up to five-fold over the summer, while the best recorded in 16 yr was an approximate doubling in numbers (Table 1)

Most previous studies on the population dynamics of northern and alpine rodents have not documented nest mortality. However, there is some indirect evidence that mortality of dependent young may be important in the dynamics of other populations as well. For example, Boonstra (1985) noted that the number of new young meadow voles (*Microtus pennsylvanicus*) trapped per lactating female was very low during a summer decline in the population, implying that mortality was very high before weaning. Similarly, Bondrup-Nielsen and Ims (1988) noted a lack of weaned young during a summer decline in wood lemming (*Myopus schisticolor*) populations, also implying that mortality in the nest may have been high. Age at maturity and length of the breeding season are recognized as critical parameters determining population growth rates (Tkadlec and Zejda 1998); perhaps nestling survival represents a third important factor to be considered. The general importance of nestling survival on population growth can only be determined with more studies that examine both reproductive potential and age-specific mortality in small rodents. The need for intensive demographic studies in association with studies of population dynamics cannot be overstated. Without them, the underlying mechanism behind population dynamics cannot be identified.

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