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# Population changes and limitation in the montane vole (*Microtus montanus*) in perennial old-field grasslands: insights from a long-term study

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We livetrapped populations of *Microtus montanus* from 1982 to 2003 in semiarid perennial old-field grasslands of southern British Columbia. We evaluated two, nonmutually exclusive hypotheses (H) to explain their population dynamics: first ($H_1$), that extended breeding during the summer or winter will drive the increase phase of population fluctuations; and second ($H_2$), that density-dependent depression of juvenile survival will be reflected in poor early juvenile survival during high populations. Populations on 2–3 grids of 1 ha were livetrapped at 3- to 8-week intervals in summer and winter except in 5 years of very low populations. Densities ranged from 10/ha to 250/ha. Peak densities occurred in 6 years and an extended low phase occurred from 1999 to 2003. Fluctuations of 3–4 years appeared in our populations but were not always present. Breeding occurred both in summer and winter, and the best predictor of the population growth rate was the fraction of adult females lactating in summer or winter, thereby supporting $H_1$. Juvenile production (number of juveniles/lactating female) varied greatly among years with the mean being over two times higher in low (2.41) than high (1.08) years, thereby supporting $H_2$. There was no clear correlation between population changes and either seasonal temperatures or rainfall, or any combination of these two variables, and no obvious cause of the prolonged low from 1999 to 2003. Thus, both female reproduction and juvenile production drive montane vole dynamics demographically, similar to what is found in other vole species. However, the ultimate cause of these changes remains to be tackled experimentally.

Key words: arid grasslands, demographic changes, population cycles, population regulation and limitation, small mammals

The montane vole (*Microtus montanus*) may be considered a keystone species of semiarid perennial grasslands, similar to other *Microtus* species elsewhere (Delibes-Mateos et al. 2011, 2015; Huitu et al. 2012). This microtine is a grassland specialist distributed throughout the central cordilleran region of western North America (Banfield 1974; Rose and Birney 1985). In the southern part of its range, the montane vole prefers arid short grassland in high-elevation alpine meadows, but in the northern part (southern British Columbia) it occurs at lower elevations in valley bottoms (Sera and Early 2003). Native bunchgrass, sagebrush communities, and perennial grasslands in valley bottoms are preferred habitats in the semiarid landscapes of the northwestern United States and southern British Columbia, Canada (Pearson et al. 2001). Perennial grasslands may be remnant native grasslands, abandoned croplands (“old fields”) such as forage fields and orchards, or often a mixture of these vegetation types. It is in these perennial grasslands that montane vole populations may persist, providing a prey base for a suite of predators such as short-tailed (*Mustela erminea*) and long-tailed (*Mustela frenata*) weasels, coyote (*Canis latrans*), badger (*Taxidea taxus*), and various hawks and owls. *Microtus montanus* also has been viewed as an important restoration tool, at least historically, for controlling encroaching woody shrubs in western meadowlands (Bramble and Bramble 2008).

*Microtus* populations often have multi-annual fluctuations in abundance in northern latitudes of Eurasia and North America, with a peak every 2–5 years, but these periods may be interspersed with annual fluctuations in abundance (Korpimäki and Krebs 1996; Krebs 2013). The montane vole is most closely related to the meadow vole (*M. pennsylvanicus*—Conroy and Cook 2000), a very well-studied species in which many of the populations undergo pronounced multi-annual cycles (e.g., Indiana—Krebs et al. 1969; Ontario—Boonstra 1985; Manitoba—Mihok 1985). There are several mechanisms potentially driving these population cycles, including behavioral changes, disease, dispersal, food supply, maternal programming, and predation (Krebs 1996, 2013; Boonstra et al. 1998). In general, studies on *M. montanus* either have been short-term (1–3 years, 1 or 2 population estimates per year—Hoffmann 1958; Murray 1965; Fitzgerald 1977; Negus et al. 1977; Pinter 1986); long-term but low intensity (1 or 2 samples per year; 10–19 years—Randall and Johnson 1979; Pinter 1988); or longer term (8 years) in atypical habitat (Negus et al. 1986). Thus, there is a dearth of long-term (≥ 10 years) detailed studies of population dynamics in grassland. In all of these, there was no attempt to determine the causal mechanisms driving population change. In contrast, only one study tackled this—predation (Maron et al. 2010) and found some impact of mammalian predators on montane vole populations.

We report here on a 17-year data set (1982–2003) with multiple sampling periods each summer and winter, of changes in abundance and demography of *M. montanus* in the semiarid perennial grasslands of southern British Columbia, Canada. Our objectives were to: (1) describe their population dynamics, and (2) based on work with other microtine populations, evaluate two hypotheses (H) to explain them: ($H_1$) that extended breeding during summer or winter will correlate with the increase phase of population fluctuations; and ($H_2$) that density-depentent inhibition of maturation of juvenile voles will be reflected in a poor index of early juvenile productivity during high populations. Recent major reviews examining the mechanisms behind microtine demography were considered (Boonstra and Krebs 2012; Krebs 2013; Oli 2019) to give insight into our nonexperimental study. A third objective was to determine the role of remnant perennial grasslands in helping to conserve this keystone species in the Okanagan Valley.

## MATERIALS AND METHODS

*Study area and design.*—Our study was located in the Okanagan Valley near Summerland, British Columbia, Canada (49°34′N; 119°40′W) in perennial old-field grasslands at an elevation range of 400–464 m. These fields were perennial hay fields abandoned about 25 years ago prior to the start of our trapping, all with similar soil profiles (Fig. 1). Vegetation was dominated by crested wheatgrass (*Agropyron cristatum*), Kentucky bluegrass (*Poa pratensis*), quack grass (*A. repens*), downy brome (*Bromus tectorum*), alfalfa (*Medicago sativa*), and herbs such as yellow salsify (*Tragopogon dubuis*), great mullein (*Verbascum thapsus*), American vetch (*Vicia americana*), prickly lettuce (*Lactuca serriola*), tall tumble-mustard (*Sisymbrium altissimum*), and diffuse knapweed (*Centaurea diffusa*). These sites each were 2–3 ha in area, within a 400-ha mosaic (Fig. 2) of tree fruit orchards, vineyards, big sagebrush (*Artemisia tridentata*), rabbit brush (*Chrysothamnus nauseosus*), bluebunch wheatgrass (*A. spicatum*), balsamroot (*Balsamorhiza sagittata*), and ponderosa pine (*Pinus ponderosa*) forest in the Bunchgrass and Ponderosa pine biogeoclimatic zones (Meidinger and Pojar 1991). Temperature and precipitation records for the general area for 1980–2003 are provided in Supplementary Data SD1 and SD2.

In June 1982, we set up trapping grids in two perennial grassland sites; additional grids were added through time (1997 and 1999) with generally 2 or 3 replicate sites being monitored simultaneously to investigate the dynamics of *M. montanus* populations. The sites were separated by a mean (± *SE*) distance of 479 ± 169 m (range of 150–1,200 m) and there were few movements of voles among sites.

*Montane vole populations.*—Populations were livetrapped at 3- to 4-week intervals annually during summer (March to October) and at 4- to 8-week intervals during winter (November to February) from 1982 to 1987 and 1993 to 2003. Sampling was not done during winter 1986 – 1987, summer 1995, winter 1995 – 1996, summer 1998, and winters 1998 – 1999, 1999 – 2000, and 2000 – 2001. Each trapping grid (1 ha) had 49 (7 × 7) trap stations at 14.3-m intervals. One Longworth live trap was placed at each station. Additional live traps were added at each station during high populations. Traps were left permanently in place between trapping sessions. Traps were supplied with whole oats and carrot, with cotton as bedding. In summer, each trap had a 30-cm × 30-cm plywood cover for protection from sunlight (heat) and precipitation. In winter, snow conditions (up to 30-cm depth) required we use trap chimneys (Merritt and Merritt 1978). These were an inverted 10-liter plastic bucket with the top removed and the bucket covered with the plywood board at each trap station. Holes were cut in the side of the bucket at ground level to give voles access to live trap(s) placed inside the bucket. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, then locked open between trapping sessions. During very warm conditions, traps were closed during the day and reset each evening. All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed using Pesola spring balances, and capture coordinates recorded. Reproductive condition in males was determined by testes position (scrotal or abdominal) and in females by the presence of lactating tissue (present or absent based on nipple size and appearance) and obvious pregnancy (Krebs et al. 1969). A pregnancy was considered successful if a pregnant female captured in 1 month was recaptured lactating in the following month. Animals were released on the grids immediately after processing. All handling of animals followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2016) and the Animal Care Committee, University of British Columbia. Seasons were defined as summer (March to October) when most breeding voles were captured and winter (November to February) when few breeding voles were captured. Except in some years, few voles bred during July and August. Thus, there were 13 summer and 11 winter periods that each had at least three trapping sessions.

*Demographic analysis.*—Abundance estimates of voles were derived from the Jolly–Seber (J–S) stochastic model for open

**Fig. 1.**—Photograph of perennial grassland with a mixture of forage and forb species at the Summerland Research Station, southern British Columbia, Canada. Photo by T. Sullivan.

populations with small sample size corrections (Seber 1982; Krebs 1999). Population size of voles (males, females, and totals) was estimated for each sampling grid and trapping period (sample time *t*) throughout the study based on the relationship of Jolly (1965):

$$\text{Population size} = \frac{\text{Size of marked population}}{\text{Proportion of voles marked}}$$

The proportion of voles marked is estimated as:

$$\alpha_t = \frac{m_t + 1}{n_t + 1}$$

where $m$ = number of marked voles captured in sample $t$; $n$ = total number of voles (marked and unmarked) captured in sample $t$; the (+ 1) is a correction for bias in small samples (Seber 1982).

With an estimated size of the marked population just before sample time $t$ that incorporates marked voles actually captured + marked voles present but not captured in sample $t = M_t$

$M_t$ = estimated size of the marked population just before sample time $t$

Estimated population size of voles: $N_t = \dfrac{M_t}{\alpha_t}$

where $N_t$ = estimated population size of voles just before sample time $t$.

We calculated the effective trapped area for each grid based on mean maximum distance moved (MMDM) by *M. montanus* between trapping periods. A buffer of one-half the value of the MMDM was added to the grid size and used to estimate the total area within which populations were sampled (Wilson and Anderson 1985). Estimates of population size were converted to a density estimate by dividing population estimates for each trapping period by the overall mean (± *SE*) effective trapped area which was 1.05 (± 0.03) ha with a range of 0.94–1.26 ha. We consider this estimate a "density index" (Krebs et al. 2011). Jolly trappability was calculated according to Krebs and Boonstra (1984).

Montane voles were classified as juvenile or adult by body mass (juvenile ≤ 26 g, adult ≥ 27 g). Measurements of recruitment (new animals that entered the population through reproduction and immigration), number of lactating females (successful pregnancies), and early juvenile productivity were derived from the sample of animals

**Fig. 2.**—Photograph of the mosaic of perennial grassland sites, tree fruit orchards, vineyards, and natural habitats at the Summerland Research Station, southern British Columbia, Canada. Grassland sites indicated by solid circles and arrows. Photo by T. Sullivan.

captured in each trapping session and then summed for each breeding period. Early juvenile productivity is an *index* relating recruitment of young into the trappable population to the number of lactating females (Krebs et al. 1969). This index is not a survival rate and is calculated as number of juvenile voles captured in each breeding period divided by the number of lactating females caught in that period. Mean total survival rates (28-day) of all voles in the trappable population for summer and winter were estimated from the J–S model.

Total survival rates of voles at 28-day periods (males, females, and totals) were estimated by:

$$\Phi_t = \text{Probability of survival of voles from sample time } t \text{ to sample time } t+1$$

$$= \frac{\text{Size of marked population at start of sample time } t+1}{\text{Size of marked population at end of sample time } t}$$

As per Krebs (1999), the marked population is added to during each sampling time as new voles are marked and released. The size of the marked population at the end of sample *t* consists of the marked individuals alive at the start of *t* plus the new individuals marked during sampling time *t*:

$$\Phi_t = \frac{M_{t+1}}{M_t + (s_t - m_t)}$$

where $s_t$ = total number of voles released after sample *t*; $m_t$ = number of marked voles captured in sample *t*.

This probability of survival is determined by sampling the marked population of voles only. Emigration of individual voles is counted as losses the same as individuals that die (Krebs 1999).

*Statistical analyses.*—Comparison of the demographic responses of *M. montanus* in high and low population years was done with mean values and 95% confidence intervals (*CI*s). To determine the possible effect of several factors on population growth rate, we conducted the following correlation analyses. We used the population growth rate over each of the 24 seasons for which we had adequate data as the dependent variable and for seasonal temperature (spring, autumn), seasonal rainfall (summer, winter), average population density (summer, winter), and percentage of adult females lactating (summer, winter), for a total of eight independent explanatory variables. All correlations reported are Pearson correlations. All statistical analyses were carried out in NCSS 20 (www.NCSS.com). The level of significance was $P \leq 0.05$ (Zar 1999).

## Results

We undertook 157 trapping periods from June 1982 to March 2003 on the sampling grids for a total of 40,670 trap-nights. The total number of individual *M. montanus* captured was 5,068. Other small mammal species regularly captured were deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*). Occasional captures included northwestern chipmunks (*Neotamias amoenus*), long-tailed voles (*M. longicaudus*), Great Basin pocket mice (*Perognathus parvus*), and vagrant shrews (*Sorex vagrans*). Overall mean (± *SE*) trappability (likelihood of capture on any given trap-night) estimate of *M. montanus* was 71.2% ± 3.4 (range 55.8–96.8%).

Overall mean number for autumn–early winter over the study was 95.7 ± 22.7 montane voles per ha (*n* = 13 ± *SE*). In terms of identifiable phases of multi-annual population fluctuations of *M. montanus*, when data were available for autumn–early winter (e.g., October to December) for 13 of 21 years, there were 6 years (1983, 1984, 1987, 1994, 1996, and 1997) of relatively high "peak" numbers, and 7 years (1982, 1985, 1993, 1999–2002) of "low" ones (Fig. 3). In five of the high years (1983, 1984, 1994, 1996, and 1997) montane voles reached estimated mean peaks of 143, 126, 225, 254, and 130 animals per ha, respectively. The high year in 1987 (143 voles per ha) occurred in September. During the low years overall, mean late autumn numbers were 9–73 voles per ha. Mean (± *SE*) peak abundance per ha in the six high years was 170.4 ± 22.4 and in the seven low years 31.6 ± 8.8, respectively. These values had nonoverlapping *CI*s: high years, 112.7 – 228.1; low years, 10.1 – 53.1. In the extended low 5-year period (1999–2003), mean (± *SE*) annual peak abundance ranged from 9.0 ± 9.0 to 43.2 ± 10.9 voles/ha (Fig. 3). Mean numbers of voles declined dramatically after the cessation of breeding in each of the high years 1983, 1984, 1987, 1994, 1996, and 1997 (Fig. 3). In addition, there were brief declines in vole abundance (%) during the summer months of July and August, and sometimes in September in 1983 (15.9%), 1984 (12.7%), 1985 (29.8%), 1987 (52.7%), 1994 (17.9%), and 1996 (48.4%) (Fig. 3).

*Demographic responses.*—Reproductive performance of *M. montanus* was measured by mean length of breeding seasons, mean number and percentage of adult females lactating, and mean number of recruits per trapping period between periods of "high" and "low" numbers of voles (Table 1). These measurements were averaged over the entire summer (March to October) regardless of a temporary decline in pregnancy rate during July and August in all years but 1983. Based on the presence of

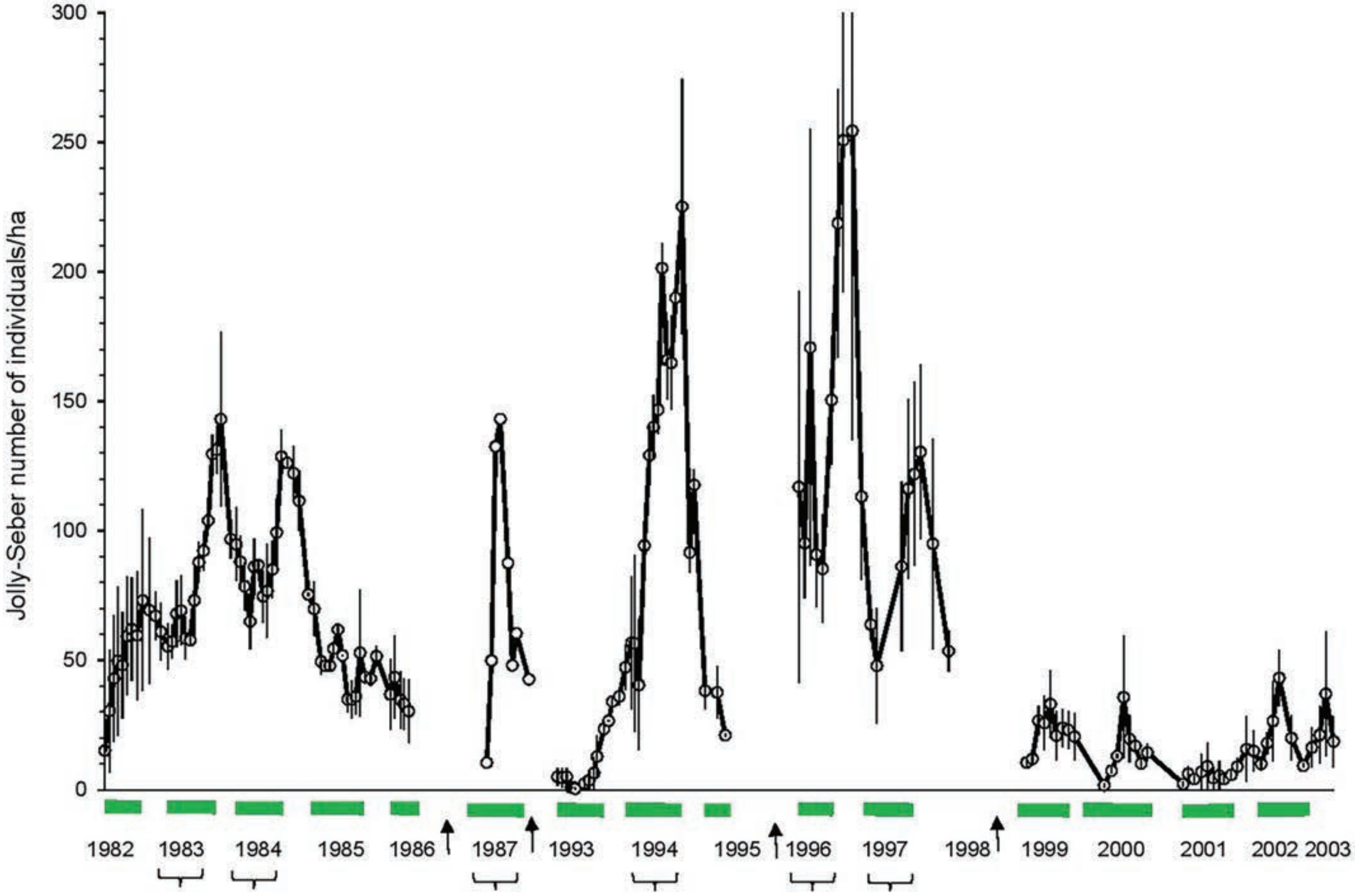

**Fig. 3.**—Mean (*n* = 2 or 3 replicate sites ± *SE*) number of *Microtus montanus* per ha as an index based on Jolly–Seber population estimates and effective trapped area, 1982–2003, in perennial grasslands in southern British Columbia, Canada. Data points indicate individual trapping weeks in summer (March to October) and winter (November to February) periods. Summer breeding periods are indicated by the green shaded bars. Years of "high" abundance are indicated along x-axis. Arrow indicates years and periods when we did not sample populations.

**Table 1.**——Mean ($n$ = 2 or 3 replicate sites) ± *SE* estimates of demographic responses of *Microtus montanus* over 13 of 21 years in perennial grasslands in southern British Columbia, Canada. High years include 1983, 1984, 1987, 1994, 1996, 1997; low years include 1982, 1985, 1993, 1999–2002. Recruits are number per trapping period. J–S = Jolly–Seber.

| Parameter | High years | Low years | Overall |
|---|---|---|---|
| Length of breeding season (weeks) | 28.2 ± 2.1 | 20.6 ± 4.4 | 24.1 ± 2.7 |
| Total number of lactating females[a] | 118.6 ± 23.0 | 26.7 ± 12.4 | 69.1 ± 17.9 |
| Summer (March to October) | | | |
| Total recruits[a] | 33.9 ± 4.1 | 10.9 ± 2.4 | 21.5 ± 4.0 |
| Juvenile recruits[a] | 9.4 ± 1.4 | 3.2 ± 0.7 | 6.1 ± 1.1 |
| Winter (November to February) | | | |
| Total recruits[a] | 37.1 ± 4.5 | 17.2 ± 3.1 | 27.1 ± 4.0 |
| Juvenile recruits | 14.2 ± 2.2 | 6.1 ± 1.4 | 10.2 ± 1.7 |
| Index of early juvenile productivity (no. juveniles per lactating female) | 1.08 ± 0.30 | 2.41 ± 0.45 | 1.80 ± 0.33 |
| Summer J–S total survival[a] (rate per 28 days) | 0.75 ± 0.02 | 0.61 ± 0.03 | 0.67 ± 0.03 |
| Winter J–S total survival (rate per 28 days) | 0.68 ± 0.05 | 0.66 ± 0.05 | 0.67 ± 0.03 |
| Number of years | $n = 6$ | $n = 7$ | $n = 13$ |

[a] Nonoverlapping 95% *CI*s between high and low years.

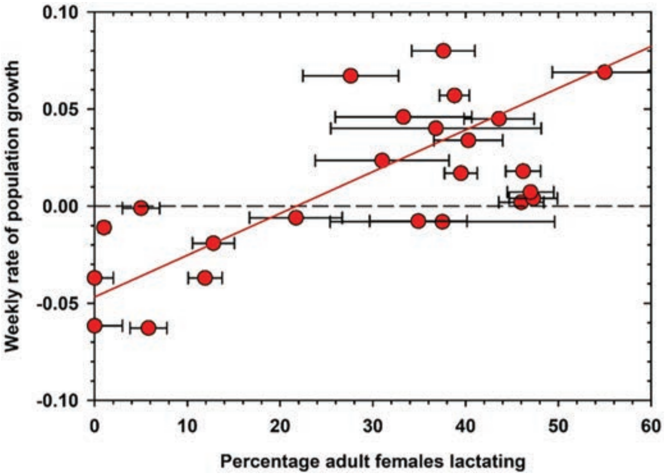

**Fig. 4.**—Relationship of seasonal rate of population growth to the percentage of lactating females (± *SE*) of *Microtus montanus* 1982–2003, in perennial grasslands of southern British Columbia, Canada. Data points are seasonal (summer, winter) averages of lactation rate in relation to the average rate of population growth ($r$) over that season, geometric mean regression, $r = 0.52$; $P < 0.01$, $n = 24$.

lactating females, mean length of summer (March to October, 35 weeks) breeding seasons were 28.2 ± 2.1 weeks in high years and 20.6 ± 4.4 weeks in low years. In terms of nonoverlapping 95% *CI*s (Table 1), *M. montanus* had 4.4 times more lactating females in high than low population years (Table 1). Vole breeding continued at a low rate through the mid-summer months (e.g., July to August) of 1983 leading to a peak population later that year but few females were lactating at that time in all other summers. There was an 18-week breeding season in the 1993 – 1994 winter in both replicate populations (October to March and into the spring) leading to a peak population later that year (Figs. 3 and 5). There was some indication of winter breeding in 1996 – 1997 and 1997 – 1998 that likely contributed to the high population in late 1997 but we have no data for a similar period in late 1998 (Fig. 5). Incidence of breeding via lactating females was 10 – 20% lower in the 2000 and 2001 summer seasons than in previous years. The proportion of lactating females in a given season appeared to be a partial predictor of the population growth rate (Fig. 4, $r = 0.52$; $P < 0.01$).

Females produced more juvenile (2.9 times) and total (3.1 times) recruits per trapping period in high than low years during the March to October breeding periods (Table 1). This pattern also occurred in winter periods for mean total recruits but was not different (overlapping 95% *CI*s) between high and low years for juvenile recruits. However, the mean (± *SE*) index of early juvenile productivity was 2.2 times higher in low (2.41 ± 0.45) than high (1.08 ± 0.30) years (Table 1; Fig. 6).

Mean total winter survival rates were similar in periods of low and high abundance (Table 1; Fig. 7). However, mean (± *SE*) total summer survival of voles was 0.61 ± 0.03 per month in low years and 0.75 ± 0.02 per month in high years. Mean monthly summer survival was consistently higher than, or similar to, winter survival throughout the study (Fig. 7). In all cases, all populations when high declined during the following breeding season and into the subsequent winters (Fig. 3).

Only one correlation with seasonal population growth rate was statistically significant: percent females lactating ($r = 0.52$; $P < 0.01$; $n = 24$). We used NCSS All Possible Regressions protocol in an unsuccessful attempt to determine if we could predict seasonal population growth rate with all possible combinations of current and 3-month lagged temperature and rainfall measurements. Neither seasonal temperature nor summer rainfall were correlated with the summer population growth rate for the whole time series nor for only the years of low numbers from 1999 to 2003. All $r$ values were less than 40% and none were significant.

## DISCUSSION

We report an intensive, long-term trapping program of montane vole populations in the semiarid grasslands of southern British Columbia. Our populations showed initial evidence of population cycling for the first 16 years, but then fell to low density annual cycles for the last 5 years. There were peak densities up to 250/ha in 6 years, low populations in 7 years, and an extended period of low numbers from 1999 to 2003. Fluctuations of 3 – 4 years appeared in our *M. montanus* populations but were not always present. Breeding occurred both in summer and winter, and the best predictor of the population growth rate appeared to be the proportion of lactating females in summer or winter. Percentage of lactating females was also related to temperature. Juvenile productivity varied greatly among years with the mean index of early juvenile productivity being 2.2 times higher in low than high population years (2.41 versus 1.08/lactating female, respectively).

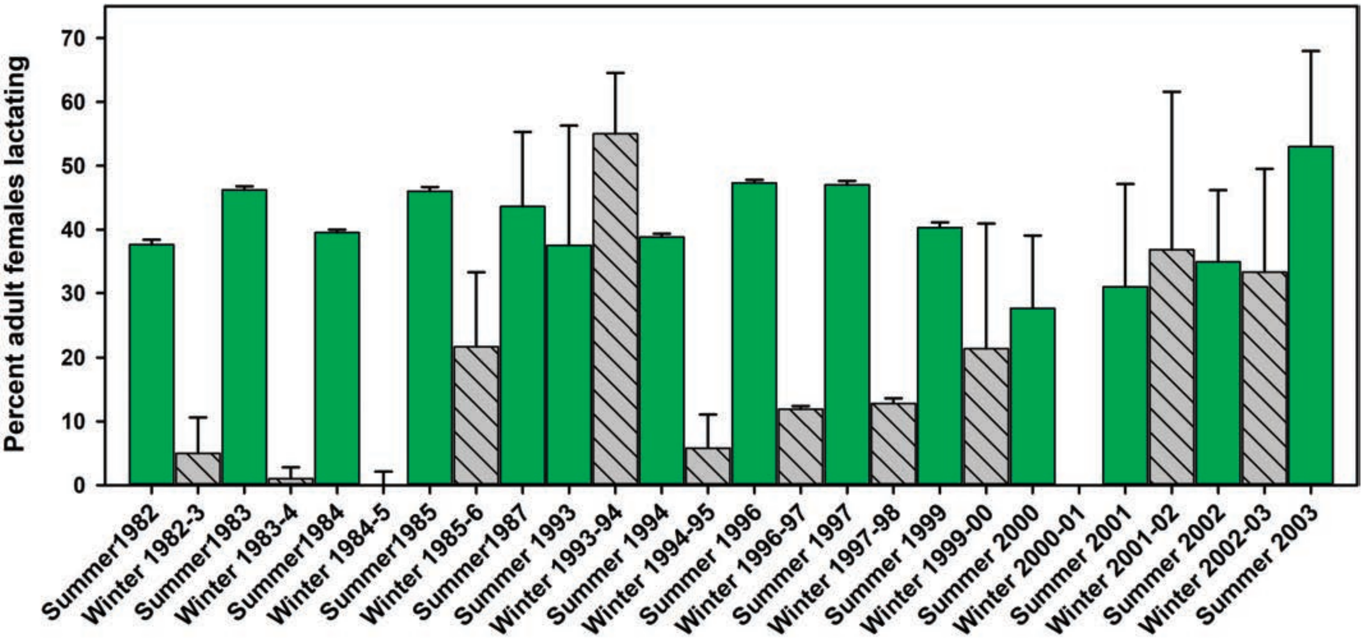

**Fig. 5.**—Summer and winter changes in the mean percentage of lactating females (successful pregnancies) for *Microtus montanus* 1982–2003, in perennial grasslands of southern British Columbia, Canada. Summer season is green, winter is gray with stripes. Note the high variation in the fraction of breeding females in different winters.

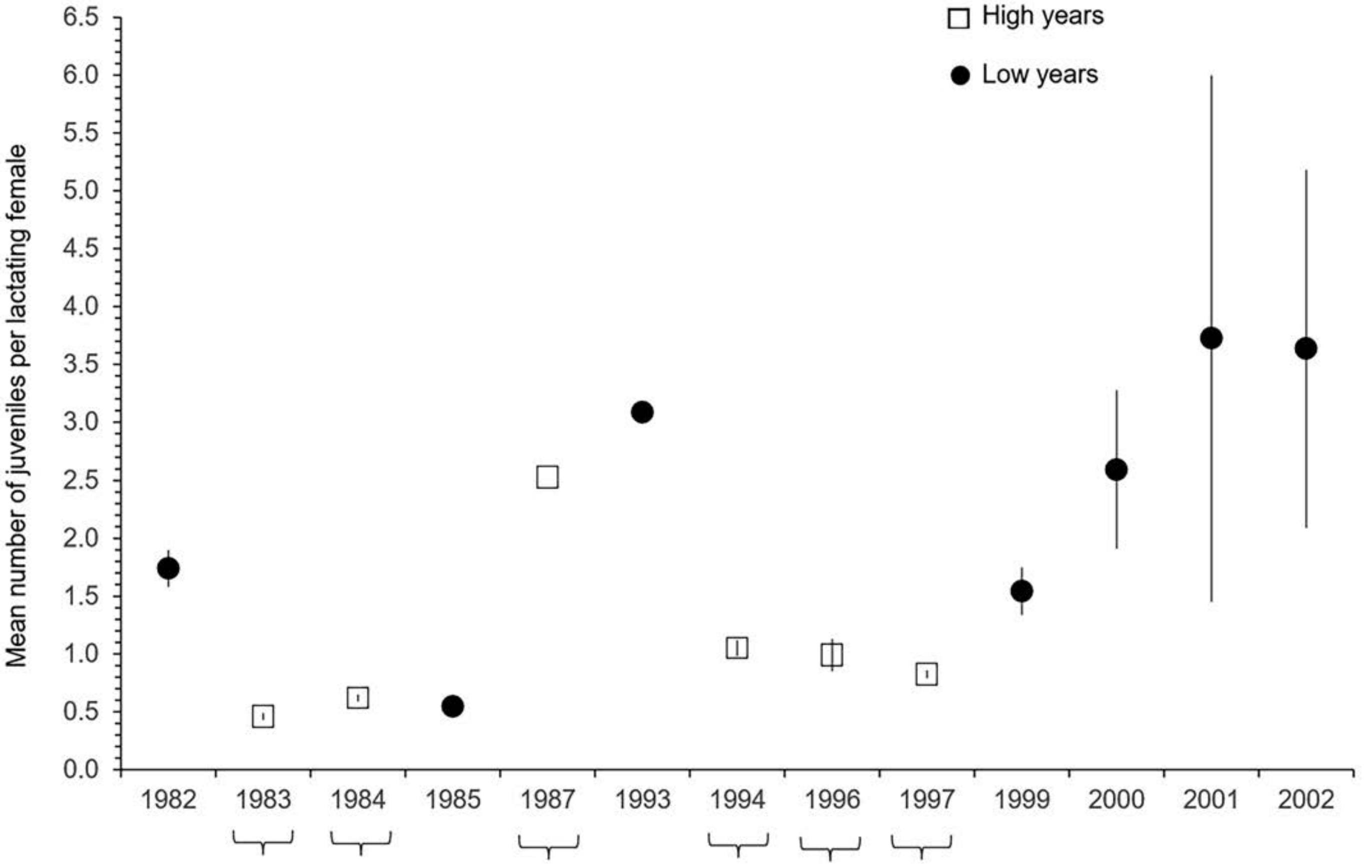

**Fig. 6.**—Mean index of early juvenile productivity (± *SE*) (number of juveniles/lactating female) for *Microtus montanus*, 1982–2003, in perennial grasslands of southern British Columbia, Canada. Years of "high" abundance are indicated along x-axis.

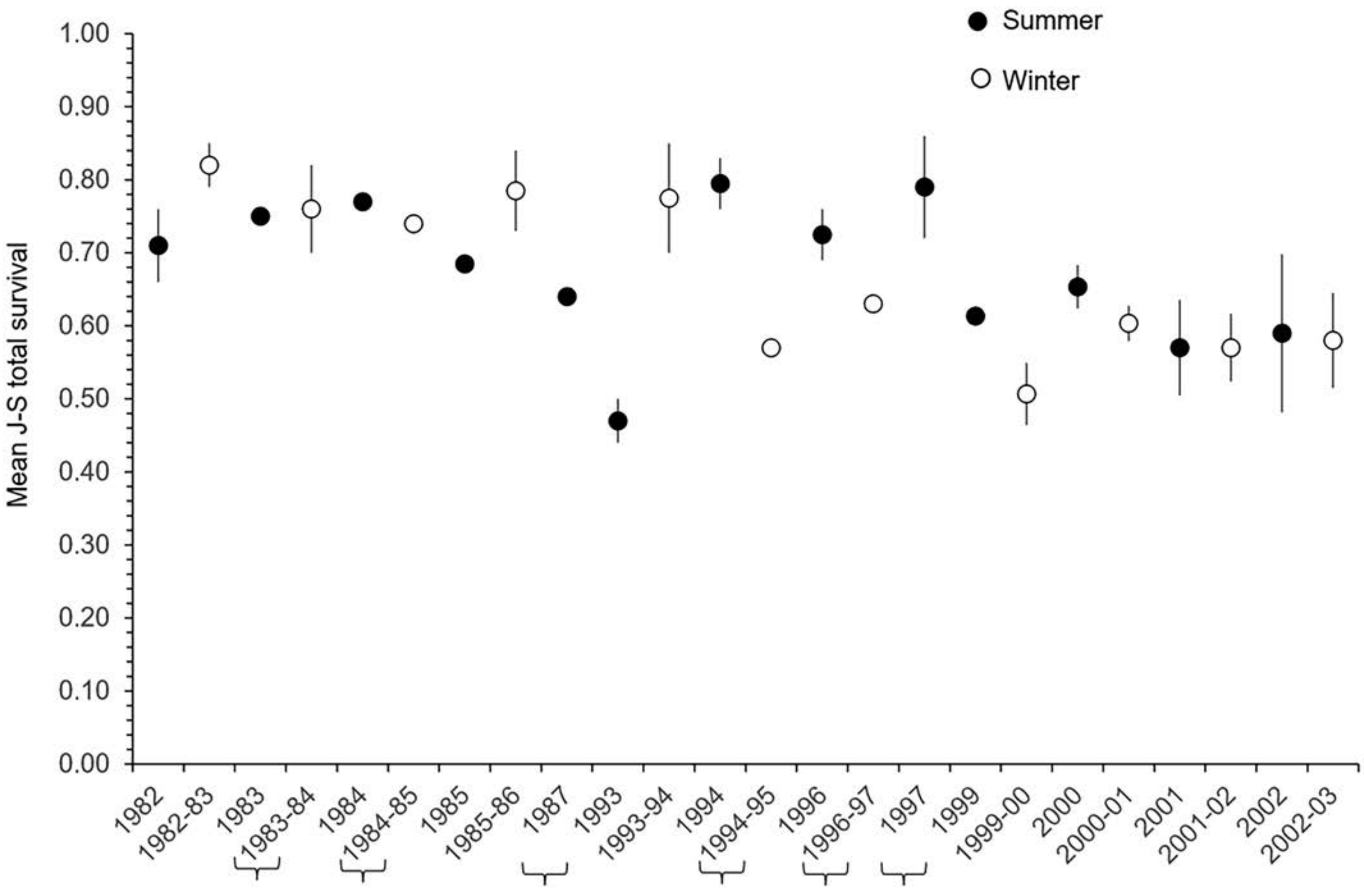

**Fig. 7.**—Mean Jolly–Seber total survival estimates (± *SE*) for livetrapped populations of *M. montanus* in seasonal summer and winter periods each year, 1982–2003, in perennial grasslands of southern British Columbia, Canada. Years of "high" abundance are indicated along x-axis.

There was no clear correlation of population changes with seasonal temperatures or precipitation and thus no suggestion that weather variables drove the population dynamics of this population. The causes of the population changes cannot be explained without concurrent experimental manipulations of predators, food, cover, and social interactions. We described here the statistical patterns without a detailed explanation of why they occurred.

There is some limited evidence from the literature suggesting that *M. montanus* has both multi-annual and annual fluctuations in natural habitat, but virtually all of these reports are based on very limited sampling (once or twice per year, sometimes with snap-trapping, some with livetrapping) and from these it is impossible to assess detailed patterns, cause, and effect. Survey records of montane voles on index lines over a 20-year period in montane meadows in northeastern California indicated fluctuations in relative abundance at approximately 3- to 5-year intervals (Hoffmann 1958; Murray 1965; Fitzgerald 1977). *Microtus montanus* populations seemed to display a 3-year periodicity in relative numbers in grass habitats in Washington State (Randall and Johnson 1979) and Montana (Maron et al. 2010). Pinter (1986, 1988) reported that *M. montanus* had multi-annual fluctuations (four peaks and four troughs) in abundance in montane meadows in northwestern Wyoming over a 19-year period sampling once per year. Peak numbers ranged from 6 to 9/100 trap-nights and low numbers < 2/100 trap-nights. However, Pinter (1986, 1988) used removal trapping once per summer which may have compromised dynamics of the one population studied. Negus et al. (1977, 1986) reported both annual and multi-annual fluctuations in abundance of *M. montanus* in Wyoming and Utah.

*Evaluation of the extended breeding hypothesis.*—Our $H_1$ that extended breeding during the dry summer or winter will correlate with the increase phase of population fluctuations was supported with winter breeding leading to a population peak in 1994. The proportion of lactating females in a given season was a partial predictor of the population growth rate. Some degree of winter breeding and increases in abundance have been recorded for *M. montanus* in high-elevation meadows and for other species of voles and lemmings at various locations with both variable and deep snowpack conditions (Jannett 1984; Millar 2001). Winter breeding leading to a long reproductive season seems to lead to an increase in numbers and often a peak population of voles particularly in temperate climates (Krebs et al. 1969; Krebs and Myers 1974). A similar case of "off-season" breeding during population increases was reported for the California vole (*M. californicus*), which normally breeds during a rainy Mediterranean winter but not during the dry late summer and early fall months (Hoffmann 1958; Krebs 1966). However, breeding during the summer dry season was sometimes extensive during the population increase phase and may be directly comparable to winter breeding (Krebs 1966; Jannett 1984).

Negus et al. (1977) reported that montane voles had variable responses to annual heterogeneity in resource availability in montane meadows. Densities in low years of < 8/ha and sometimes high densities near 80/ha occurred in rich patches of habitat. Conversely, Negus et al. (1986) described noncycling annual fluctuations of *M. montanus* over 8 years in a marsh environment at lower elevation sites, where August densities consistently reached 370 – 555 voles/ha. Spring numbers in April ranged from 124 to 296 voles/ha. Thus, in a seasonally simple and highly predictable environment with respect to climate and one major grass species (*Distichlis stricta*), *M. montanus* populations did not show large-scale multiyear density fluctuations, but rather showed only annual fluctuations (Garsd and Howard 1981; Negus et al. 1986). Negus et al. (1986) predicted that in such stable environments, extrinsic factors such as climate and predation may exert a primary regulatory influence on microtine populations. However, we found only a weak relationship between seasonal temperature and population change. We suggest that the key driver of their demography in the salt marsh was the lack of complexity of the species diversity of the vegetation—it was a boom and bust system—and thus atypical relative to normal montane habitats.

*Evaluation of the juvenile productivity hypothesis.*—$H_2$ predicted that density-dependent inhibition of maturation and survival of juvenile voles will be reflected in poor early juvenile productivity during high populations. This hypothesis seemed to be supported because juvenile productivity was substantially higher in low than high populations of *M. montanus*, hence was a second key component of population changes. The key driver of juvenile survival in *Microtus* populations in good quality habitat is female territoriality (Boonstra 1978, 1984). Social strife among adult and juvenile voles could lead to physiological changes that affect reproduction and survival (Boonstra 1985). As reviewed by Boonstra and Krebs (2012) for red-backed voles *Myodes* and other microtine populations, with just 1 – 2 population estimates it is difficult to determine the demographic mechanisms driving population change in the spring to early summer, when breeding and social reorganization may be dominant factors. This difficulty also holds at the start of winter when conditions are poor for rodents with respect to lack of snow cover and vulnerability to predation. As noted by Hansen et al. (1999), a causal feature of population change, such as winter mortality, may be indistinguishable from socially induced mortality (e.g., negative interactions between adults and juveniles) or dispersal in springtime (Krebs and Boonstra 1978). Changes in abundance during summer or winter breeding seasons are essentially impossible to measure without multiple estimates (i.e., several sampling periods) of population dynamics during these periods. Studies with multiple population and breeding estimates may be able to identify density-dependent inhibition of maturation and survival of juvenile voles as a primary cause of a population decline in a given breeding season (Boonstra and Krebs 2012).

We suggest an alternative explanation to be the fence effect, the dynamics expected when dispersal is prevented (Krebs et al. 1969; Tamarin et al. 1984). The location of our perennial grassland sites within the mosaic of managed and those natural habitats unfavorable to montane voles may have simulated a "fence effect" by limiting dispersal possibilities for voles. The only alternative suitable habitats for voles at our study area were some of the field edges and hedgerows bordering orchards and vineyards that had sufficient cover of herbaceous vegetation (Sullivan and Sullivan 2009).

Major predator species that likely preyed upon montane voles during our study included coyotes, hawks, owls, and gopher snakes (*Pituophis melanoleucus*). Although we have no quantitative data, these predators were observed on various occasions throughout the 17 years of monitoring vole populations. Coyotes were particularly prevalent during the low population years of 1999 – 2003. Weasels were rare during the overall study.

Another possibility for the low abundance of *M. montanus* in 1999 – 2003 may be similar to the damping out or collapsing of microtine population cycles over at least the last three decades, particularly in northern Europe (Ims et al. 2008). Environmental factors such as stochasticity (Stenseth 1999), fragmentation of source habitats (Christensen and Hornfeldt 2003), and climate change (Ims et al. 2008) have been advanced as possible explanations. The latter two factors may be particularly germane to our extended low numbers of *M. montanus* in the 1999 – 2003 period. Reduced winter population growth was demonstrated by Cornulier et al. (2013) as a cause for dampening of multi-annual cycles of several European vole species, and that process was also observed in our *M. montanus* populations during the 5 years of low numbers. Population fluctuations of *M. pennsylvanicus* also may have been damped in temperate and boreal forests of the Pacific Northwest (PNW) of North America. One anthropogenic cause might be the reductions in plant community abundance and structure from cattle (*Bos taurus*) grazing during summer in early successional forest habitats (Sullivan and Sullivan 2010, 2014).

Finally, given that weather is unlikely to be the explanation for the 5-year low, an alternative hypothesis is the appearance of a new disease or parasite. We have no evidence for this and so present it as a hypothesis. However, an analogous situation occurred in the boreal forests of southwestern Yukon in the deer mouse (*P. maniculatus*—Krebs et al. 2018). Small mammals have been continuously livetrapped there from 1976 to the present. Deer mice were the second most abundant small mammal in this community until the fall of 1989, when they simply disappeared and not one was caught on the trapping grids for the next 6 years. They finally returned in 1996, but at lower numbers. Krebs et al. (2018) ruled out changes in food abundance, predators, and small mammal competitors. Thus, the appearance of a new disease or parasite was a possibility and so too in the montane vole (see Ostfeld 2008 for conceptual models for their potential role in small mammal population dynamics).

*Management and conservation.*—In terms of seasonally rich habitats, the montane vole occasionally has been a major herbivore pest in valley bottom ecosystems, sometimes irrupting in populations capable of serious feeding damage to agricultural crops. According to Murray (1965) and Getz (1985), population outbreaks of *M. montanus* in 1906 – 1909 and 1957 – 1958 were the greatest on record in western US croplands, particularly forage such as alfalfa, with maximum densities estimated over 1,000 per ha or more, respectively. In some inland areas of the PNW of North America, montane voles also may feed on fruit trees during winter where suitable grassland habitat is nearby or within the orchard habitat (Godfrey 1986; Sullivan and Hogue 1987; Askham 1988).

The montane vole could be considered a keystone species, similar to other species of *Microtus* and *Myodes*, despite its historical reputation as a crop-damaging pest (Delibes-Mateos et al. 2011). By being a prey species for a suite of predators and feeding on various plant parts and seeds, along with their runway and burrow activities, voles help to distribute seeds and fungal spores essential to plant production (Sera and Early 2003; Maser et al. 2008). There is less than 10% of the semiarid inter-montane grasslands in the PNW that have not suffered some degree of habitat losses owing to agricultural (including cattle grazing), urban, and recreational developments (Harper et al. 1993; Fleischner 1994; Pearson et al. 2001). Linear noncrop habitats with old-field vegetation attributes may provide some sites for maintenance of *M. montanus* populations (Sullivan et al. 2012).

*Conclusions and future research.*—The pattern of population change in *M. montanus* was one of being cyclic for the first 12 years of the study and then changing to 5 years of an annual pattern of low numbers. The cyclic pattern was similar to that previously described for *M. pennsylvanicus* (Krebs et al. 1969; Boonstra 1985; Mihok et al. 1985; Getz et al. 2005), *M. townsendii* (Lambin and Yoccoz 2001), *M. oeconomus* (Aars and Ims 2002), and the brown lemming, *Lemmus sibiricus* (Fauteux et al. 2015). Seasonal population growth was variable but successful autumn or winter breeding was a key element of rapid population increase to peak numbers. Mortality of juveniles also was variable but we do not know the causes of loss in our populations. Fluctuations of 3–4 years are common in *M. montanus* but not always present. The detailed causes of the changes in demography await experimental manipulations.

We have focused on the demographic drivers of population change in this study. To determine the causal factors regulating the population fluctuations of *M. montanus*, we need rigorous, large-scale, year-round field experiments testing various hypotheses. The two key questions that should be focused on now are the mechanisms behind variable winter breeding and the highly variable rate of juvenile survival. The roles of food, predation, breeding season reorganization, and dispersal require experimental manipulation to determine the mechanisms driving population change in this keystone species. Breeding season reorganization needs to investigate the changing degree of juvenile breeding and survival during various phases of a population fluctuation. Relevant study areas will need to be large enough (e.g., 2–3 ha units) old-field sites that can generate substantial changes in vole abundance. This requirement may prove difficult if current loss of old-field habitat continues. For predators, we need detailed data on diets and numbers of the major vole predators in these perennial grasslands.

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## SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Penticton monthly precipitation, 1980–2003.

**Supplementary Data SD2.**—Penticton mean maximum and minimum monthly temperatures, 1980–2003.

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