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Mechanisms of population limitation in the southern red-backed vole in conifer forests of western North America: insights from a long-term study

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Our goals were to characterize multiannual population changes of the southern red-backed vole (*Myodes gapperi*) to determine potential cycling behavior, and to specify the possible causes of these changes. We analyzed a detailed, 21-year record of changes in abundance of *M. gapperi* in late successional coniferous forest in southern British Columbia, Canada, from 1995 to 2015. We evaluated 3 hypotheses (H), namely that population changes are related to: (H_1) changes in food supply from cone crops of coniferous trees; (H_2) changes in forest habitat associated with beetle-killed lodgepole pine (*Pinus contorta*) trees; and (H_3) territorial reorganization leading to breeding season declines in abundance. There were 3 cyclic population fluctuations (6- to 7-year periodicity) where red-backed voles reached mean fall numbers of 19–25, 15–16, and 26–27 per ha, respectively; in contrast, only 2–5 voles per ha occurred during population lows. Breeding season declines in abundance occurred in 17 of 21 years, with particularly precipitous drops ranging from 49% to 69% loss of voles. *M. gapperi* had more successful pregnancies, juvenile recruits, and adult recruits in the high than in the low population years. Mean index of early juvenile survival was 22% higher in low than high population years. Mean summer survival (58%) was consistently lower than that in winter (83%). Population increases were positively related to cone crops of 3 coniferous tree species. Thus, H_1 was partially supported in 3 of 4 seedfall events. Positive changes in forest habitat, resulting from seed rain as a food supply and fallen debris from beetle-killed pine trees as cover, may have supported high numbers of voles in 2011–2012 (H_2). A spring reorganization event limited the number of breeding animals by density-dependent inhibition of maturation and survival of juvenile voles, and led to breeding season declines (H_3). Rigorous field experiments are needed to test these hypotheses and their interactions as mechanisms driving population change.

Key words: British Columbia, cone crops, coniferous forest, demographic changes, *Myodes gapperi*, population fluctuations, red-backed voles, spring reorganization

The southern red-backed vole (*Myodes gapperi*) is an important indicator species of closed-canopy forests in both natural and managed landscapes. This microtine commonly inhabits late successional coniferous and deciduous forests across temperate and boreal North America south of 60° latitude (Merritt 1981). They are a good candidate species for evaluation of the development of "old forest" structural attributes in young stands (Raphael 1988; Nordyke and Buskirk 1991; Pearce and Venier 2005). In addition, *M. gapperi* is a major mycophagist, consuming hypogeous ectomycorrhizal fungi and disseminating their spores in the forest environment (Maser et al. 1978, 2008). The presence of red-backed vole populations at mature or old-growth forest levels of abundance suggests that networks of food sources and predators (e.g., short-tailed weasels [*Mustela erminea*] and American martens [*Martes americana*]) may also be present. Thus, *M. gapperi* may be considered a "keystone" species of temperate and boreal forests (Thompson and Angelstam 1999). This vole is opportunistic in feeding on fungi during summer and fall, conifer seeds and berries during fall and winter months, and miscellaneous plant parts, lichens, and arthropods year-round in western late successional forests (Merritt and Merritt 1978; Merritt 1981; Gunther et al. 1983; Ovaska and Herman 1986; Lobo et al. 2009).

Much research has been conducted on voles of the genera *Microtus* and *Myodes* in Fennoscandia and North America focused on understanding the 3- to 5-year cyclic fluctuations in some populations and geographic locations (Korpimaki et al. 2005; Krebs 2013). The existence of population cycles and fluctuations and the causes for these population dynamics in *M. gapperi* and other *Myodes* species in North America were reviewed by Boonstra and Krebs (2012). *Myodes* cycled in just 2 of 7 long-term studies (at least 14 years of data), or fluctuated in abundance at irregular intervals with poor overwinter survival in most years and chronically low densities. Boonstra and Krebs (2012) considered 8 factors to help explain the differences in cyclic and irregular population fluctuations, and they concluded that food, in the form of berry crops for the northern red-backed vole (*M. rutilus*) and tree seeds for *M. gapperi*, may be sufficient. Two studies from Maine (Elias et al. 2006) and northwestern Quebec (Fauteux et al. 2015) showed 3- to 5-year cyclic fluctuations for *M. gapperi*. Elias et al. (2006) showed that peak years in abundance of *M. gapperi* coincided with high masting years of white pine (*Pinus strobus*). High vole numbers were also related to abundant black spruce (*Picea mariana*) cone crops (Fauteux et al. 2015). Black spruce is a serotinous conifer and requires fire to fully open cones for seed dispersal; heavy seed crops occur at intervals of 2 to 6 years with peak crops every 4 years (Viereck and Johnston 1990). Martell (1981) reported that conifer seeds were an insignificant part of the diet of *M. gapperi* in undisturbed upland black spruce forest in northern Ontario. However, lack of conifer seeds in diet surveys may be related to the absence of cone crops at specific times, detection issues, and geographic locations. Population dynamics of seed predators are affected by seed crop availability within a season and by the frequency of masting events, which occur synchronously over large geographic areas (Koenig and Knops 1998, 2005; Ostfeld and Keesing 2000).

Many of the long-term data sets analyzed by Boonstra and Krebs (2012) consisted of 1 or 2 population estimates per year. In those cases, it is difficult to determine the demographic mechanisms related to population change, be it at the start of winter when conditions are poor for rodents with respect to lack of snow cover and vulnerability to predation, for example, or in the spring to early summer when breeding and social reorganization may be dominant factors. Thus, a causal feature of population change could be winter mortality (Hansen et al. 1999), but this may be indistinguishable from socially induced mortality (e.g., negative interactions between adults and juveniles) or dispersal in springtime (Krebs and Boonstra 1978). A major difference between the demography of *Myodes* populations in Fennoscandia that cycle, and those in North America that apparently do not, relates to declines in abundance during the breeding season (Boonstra and Krebs 2012). This factor is almost impossible to measure without multiple estimates (i.e., several sampling periods) of population dynamics during reproductive periods. If abundance of voles declines during the breeding season, and multiple population and breeding estimates are available, then density-dependent inhibition of maturation and survival of juvenile voles may be evaluated as the cause (Boonstra and Krebs 2012).

We report on a 21-year record (5–6 sampling periods each summer) of changes in abundance and demography of *M. gapperi* in late successional coniferous forest in southern British Columbia (BC), Canada, from 1995 to 2015. Our objectives were 1) to provide a description of demographic changes in populations of *M. gapperi*; and 2) evaluate 3 hypotheses (H) that may explain population changes during this 21-year period: (H_1) cone crops of interior spruce (*Picea glauca* × *P. engelmannii*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and subalpine fir (*Abies lasiocarpa*) correspond to peak years; (H_2) changes in forest habitat and seed dispersal from mountain pine beetle (*Dendroctonus ponderosae*; MPB)-killed lodgepole pine (*Pinus contorta* var. *latifolia*) trees lead to sustained high years; and (H_3) territorial spring reorganization leads to breeding season declines in abundance.

For the food hypotheses H_1 and H_2, we predicted that increased food supply from fall masting of spruce, Douglas-fir, subalpine fir, or "seed rain," and habitat alteration from MPB-killed lodgepole pine would enhance overwinter survival of *M. gapperi*, as well as enhance reproductive output in the following summer breeding period. Therefore, red-backed vole densities should be higher in the summer and fall periods following conifer masting compared to years of low seed production. In addition, if seed-eating invertebrates attack subalpine fir seed, either in cones or post-dispersal on the forest floor, and these invertebrates provide a secondary food source for rodents such as deer mice (*Peromyscus maniculatus*) and *M. gapperi*, then delayed population increases may occur in years after a masting event of subalpine fir as suggested by Lobo and Millar (2013). For the social interaction hypothesis H_3, we predicted that territorial spring reorganization via density-dependent inhibition of maturation and survival of juvenile voles would lead to breeding season declines in abundance of *M. gapperi*.

METHODS

Study area and design.—Our study was located in the Bald Range 25 km west of Summerland, BC (49°40′N; 119°53′W) in the upper Interior Douglas-fir (IDF_{dk}; d,k = dry precipitation regime, cool temperature regime) and Montane Spruce (MS_{dm}; d,m = dry precipitation regime, mild temperature regime) biogeoclimatic zones (Meidinger and Pojar 1991). The area has sandy loam soils with gently rolling topography at 1,450 to 1,520 m elevation. The upper IDF and MS have a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0°C for 2–5 months, and above 10°C for 2–5 months, with mean annual precipitation ranging from 300 to 900 mm. Open- to closed-canopy mature forests of Douglas-fir cover much of the IDF zone, with even-aged post-fire lodgepole pine stands at higher elevations. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire 100–150 years ago. Hybrid interior spruce and subalpine fir are the dominant shade-tolerant climax trees. Trembling aspen (*Populus tremuloides*) is a common seral species and black cottonwood (*Populus trichocarpa*) occurs on some moist sites (Meidinger and Pojar 1991).

This study was located in a commercial forest landscape covering 10,000 ha and was a mosaic patchwork of various post-harvest and old-growth successional stages composed of the 4 major coniferous tree species. Parts of the study area had been partially harvested by individual tree selection and diameter-limit cutting of Douglas-fir in 1962–1964. Clear-cut harvesting of lodgepole pine with retention of dispersed (single) and aggregated (group) seed-tree reserves of Douglas-fir began in this area in 1977 in response to an outbreak of MPB and continued to 1984. MPB attacks continued and further salvage harvesting occurred in 1996 and 2016. Prior to this last harvest event, approximately 30% of uncut old-growth forest remained in this area.

There were no reports of seed availability for the study area but information was available for a wider range. Cone crops for Douglas-fir in the Pacific Northwest occur at irregular intervals with 1 heavy and 1 medium crop every 7 years on average (Hermann and Lavender 1990). White spruce (Nienstaedt and Zasada 1990) and Engelmann spruce (Alexander and Shepperd 1990) have good to heavy crops every 2 to 5–6 years. Subalpine fir has good to heavy crops every 3 years (Alexander et al. 1990). More locally, there have been 2 "heavy" and 2 "moderate" cone crops in spruce and subalpine fir, respectively, in the Okanagan-Thompson area over the 21-year period of our study (A. Vyse, pers. obs.).

For lodgepole pine, the interior province-wide MPB epidemic passed through our study area in 2008 resulting in mortality ranging from 19% to 40% in lodgepole pine stands. The overall effect on forest structure was sporadic possibly because of the greater mix of coniferous tree species, and earlier harvest of much of the lodgepole pine, in the south compared with the almost complete devastation of primarily lodgepole pine-dominated forests in north-central BC (Walton et al. 2009). MPB has been in various endemic stages in the southern interior of BC over much of the last half of the 20th century (Safranyik and Wilson 2006).

In May 1995, we installed sampling grids in 3 stands that were separated by an average (± *SE*) of 1.79 ± 0.49 km (range 0.67–2.96 km). All stands were in old-growth forest composed of a mixture of Douglas-fir, lodgepole pine, interior spruce, and subalpine fir. The latter 2 species were particularly common in wetter sites. Grids in 2 forest stands were moved in 2010 when the original forest cover was lost to blow down in one stand and almost complete MPB-induced mortality in the other stand where lodgepole pine was the dominant species. Grids were moved an average of 1.5 km from their original locations into undisturbed forest patches. Mean ages of lodgepole pine ranged from 80 to 120 years and of Douglas-fir and other conifers ranged from 120 to 220 years. Mean (± *SE*) tree heights ranged from 10.8 ± 5.9 to 19.4 ± 2.3 m for the 4 conifer species. Mean (± *SE*) density of overstory (> 3 m height) conifers was 1,402 ± 361 stems/ha and for all conifers was 2,092 ± 498 stems/ha. Overstory density (conifers > 3 m in height) was maintained at a mean (± *SE*) of 1,437 ± 386 stems/ha after moving the grids in 2010. Canopy closure ranged from 82% to 88% in these 3 forest stands, and hence understory herb and shrub layers were relatively depauperate. Pinegrass (*Calamogrostis rubescens*), racemose pussytoes (*Antennaria racemosa*), heart-leaved arnica (*Arnica cordifolia*), and one-sided wintergreen (*Orthilia secunda*) were major herb species. Sitka alder (*Alnus sinuata*), Utah honeysuckle (*Lonicera utahensis*), falsebox (*Pachistima myrsinites*), kinnikinnick (*Arctostaphylos uva-ursi*), birch-leaved spiraea (*Spiraea betufolia*), and grouseberry (*Vaccinium scoparium*) were major shrub species.

Red-backed vole populations.—Populations of *M. gapperi* were sampled at 4-week intervals annually from May to October 1995 to 2015. One livetrapping grid (1 ha) was located in each stand and had 49 (7 × 7) trap stations at 14.3-m intervals with 1 Longworth live trap at each station. Traps were baited with whole oats, a slice of carrot, and cotton as bedding. Each trap had a 30 × 30 cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and the morning of day 3, and then locked open between trapping periods. All voles captured were ear-tagged with serially numbered tags, weighed on Pesola spring balances, and breeding condition and point of capture were recorded (Krebs et al. 1969). The duration of the breeding season was noted by palpation of male testes and the condition of mammaries of the females (Krebs et al. 1969). A pregnancy was considered successful if a pregnant female captured in 1 month was recaptured lactating in the following month. Voles were released on the grids immediately after processing. All handling of animals followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and the Animal Care Committee, University of British Columbia.

Population data analyses.—Abundance estimates were derived from the Jolly-Seber (J-S) stochastic model for open populations with corrections for small sample sizes (Seber 1982; Krebs 1999). We calculated the effective trapped area for each grid based on mean maximum distance moved (MMDM) by *M. gapperi* 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 effective trapped areas which were 1.23, 1.25, and 1.37 ha for the 3 grids. We consider this estimate a "density index" (Krebs et al. 2011). Jolly trappability was calculated according to Krebs and Boonstra (1984).

Myodes gapperi were classified as juvenile (≤ 18 g) or adult (≥ 19 g) based on body mass. Measurements of recruitment (new animals that entered the population through reproduction and immigration), number of successful pregnancies, and early juvenile survival were derived from the sample of animals captured in each trapping session and then summed for each summer period (May to September). Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs et al. 1969), calculated as number of male and female juvenile voles captured each summer divided by the number of lactating females caught in that summer. Proportion of young of the year that were in breeding condition in the summer of their birth was calculated for both males and females. These voles needed to be captured initially as juveniles, be caught at least twice as residents, and be in a reproductive state in that same summer. Mean total survival rates (28-day) for summer (May to September) and winter (October to April) were estimated from the J-S model. Overwinter survival rates for 2009–2010 were not available for 2 grids that were moved to new forest stands in May 2010. Summer population growth was the Fall estimate (t)/Spring estimate (t) and winter population decline was the Spring estimate ($t + 1$)/Fall estimate (t).

Autoregressive modeling and spectral analysis.—We analyzed the time series data on fall population abundance for all 3 sites separately. We used Statistica 13.0 to calculate autocorrelation coefficients and for fitting 2nd-order autoregressive models. Following Bjørnstad et al. (1995), we log transformed population estimates for normality and fitted the autoregressive model:

$$R_t = a_0 + a_1 X_{t-1} + a_2 X_{t-2} + e_t$$

where $R_t = X_t - X_{t-1}$; $X_t = \log(N_t)$; N_t = abundance estimate for year t; t = year. The coefficients a_1 and a_2 are measures of direct density dependence and delayed density dependence, respectively.

To assist in determining if there was a cyclic periodicity in the population indices, we estimated spectral densities after detrending the data, and smoothed the resulting periodogram with a 5-point moving average based on Hamming weights (Statistica 2013).

Coniferous cone crops.—The 2 "heavy" and 2 "moderate" crops in spruce and subalpine fir over the 21-year period of our study were collected at the Sicamous Creek Silvicultural Systems Project, near Sicamous, BC (50°50′N, 119°50′W), 146 km from our study area. The forest corresponds to the Engelmann Spruce Subalpine Fir (ESSF) biogeoclimatic zone (Meidinger and Pojar 1991) and is representative of the ESSF wet cold subzone (ESSFwc2) described by Lloyd et al. (1990). The site elevation ranges from 1,530 to 1,830 m. The forest is an old-growth stand of subalpine fir and Engelmann spruce that originated approximately 300 years ago and has experienced individual tree or group mortality since the mid-1800s (Parish et al. 1999). Ten seed traps (initially 0.64 m^2 and 0.25 m^2 after 10 years) were installed in each of 3 relatively undisturbed stands in the summer of 1995. Following collection of spruce and subalpine fir seed and litter from each trap, seed was sorted from the litter. The seed fraction was further sorted into species. These were x-rayed and the number of filled seeds counted. Seed counts were converted to mass (kg/ha) values by conversions given in Leadem et al. (1997). Douglas-fir trees were not found in these stands, and hence we investigated another source of cone crop data for this tree species in the Okanagan-Thompson area (36,000 km^2). Cone collections of Douglas-fir occurred throughout the 21-year period to obtain seed for nursery production of seedlings. These data were provided by the Tree Seed Centre, BC Ministry of Forests, Lands, and Natural Resource Operations and were total amounts (kg) of filled seed collected in the Thompson-Okanagan area each year. Thus, we do not have amounts of Douglas-fir seed per ha, but rather relative overall amounts from year to year.

Within each of the genera *Abies*, *Picea*, *Pinus*, and *Pseudotsuga*, cone crops were synchronous across wide (e.g., up to 2,500 km for *Pinus*) geographic regions of the Northern Hemisphere (Koenig and Knops 1998, 2005). The heavy crops of spruce and subalpine fir during this 21-year period were widespread in southern BC based on cone surveys conducted by AV. Low and moderate size crops followed this pattern. We assume that Douglas-fir followed a similar pattern.

RESULTS

Red-backed vole populations.—We conducted 118 trapping periods from June 1995 to October 2015 on the 3 grids. The total number of individual *M. gapperi* captured was 1,683. Other forest-floor small mammal species included deer mice and occasional captures of northwestern chipmunks (*Neotamias amoenus*), montane shrews (*Sorex monticolus*), masked shrews (*S. cinereus*), and short-tailed weasels. Overall mean (± *SE*) trappability (likelihood of capture on any given trap-night) estimates of *M. gapperi* were 78.4% ± 3.6, 86.5% ± 2.4, and 87.5% ± 2.3 for the 3 grids. There were 3 identifiable population peaks of *M. gapperi* over the 21-year period with relatively high populations in 1997–1998, 2004–2005, and 2011–2012 (Fig. 1). In these 3 high periods, each separated by approximately 7 years, red-backed voles reached estimated mean fall numbers of 19–25, 15–16, and 26–27 per ha, respectively. During population lows, mean fall numbers were 2–5 voles per ha. Mean (± *SE*; $n = 6, 15$) fall abundance in high years was 21.42 ± 2.04 and in low years was 7.87 ± 1.00, respectively. These mean values had non-overlapping 95% confidence intervals (*CI*s): high years, 16.2–26.7; low years, 5.7–10.0. Mean fall densities were, on average, 2.0 times higher than those in the spring. Estimated densities of *M. gapperi* per ha in the 2nd spring of each of our 2-year population highs (1997–1998, 2004–2005, and 2011–2012) were 19.4, 8.6, and 14.7. However, numbers of voles declined during the breeding season in 17 of 21 years, but in 10 of these it was only temporary, with particularly precipitous drops ranging from 49% to 69% loss of voles in the years 1998, 1999, 2001, 2007, 2008, and 2013 (Fig. 1).

We found 2 significant time lags in fall abundances of *M. gapperi* (Table 1). Significant negative autocorrelation was identified at 4 years on 1 grid, and at 3 years overall (Table 1). For a population that exhibits a 6- to 8-year cycle, the basic configuration would be to have a positive autocorrelation at 1 year, negative autocorrelations at 3–4 years, and positive autocorrelations at 7–8 years (Turchin 2003). Our results conform to this model though not all correlations were significant (Table 1).

Autoregressive models were fit to the mean abundance of all 3 grids combined (Table 2). The lag-1 regression coefficient

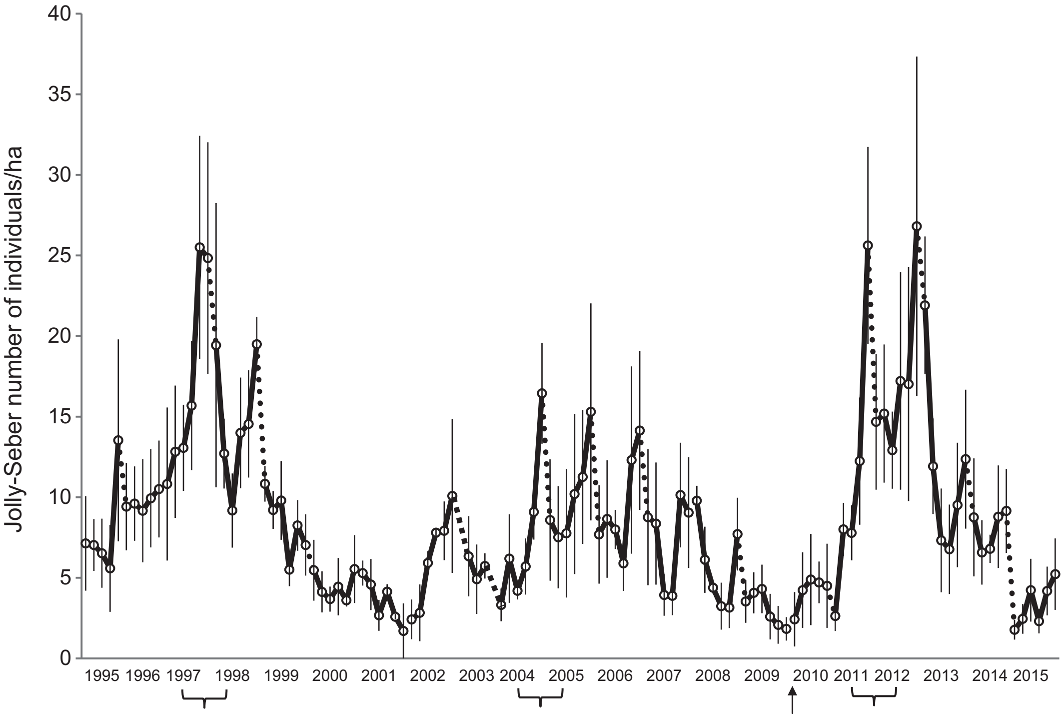

Fig. 1.—Mean (n = 3 replicate sites ± *SE*) number of *Myodes gapperi* per ha as an index based on Jolly-Seber population estimates and effective trapped area, 1995 to 2015, in old-growth forest in southern British Columbia, Canada. Data points indicate individual trapping weeks each summer (May to October) and dots indicate winter periods when we did not sample populations. Years of "high" abundance are indicated along x-axis. Arrow indicates year of grid replacement.

Table 1.—Autocorrelations of *Myodes gapperi* time series from fall abundance estimates from 3 populations in British Columbia, Canada, 1995–2015, and the combined mean population, up to lags of 9 years. Statistically significant autocorrelations are shown in bold. Significant negative autocorrelations at lag 3 or lag 4 would indicate a cycle period of 6 to 8 years.

Population	Lag 1	Lag 2	Lag 3	Lag 4	Lag 5	Lag 6	Lag 7	Lag 8	Lag 9
Grid Q	0.30	0.01	−0.38	**−0.47**	−0.26	0.00	0.13	0.24	0.16
Grid S	0.41	−0.13	−0.42	−0.16	−0.11	−0.01	0.13	0.21	0.16
Grid RZ	0.18	−0.03	−0.04	−0.20	−0.07	0.18	0.24	0.23	−0.13
Mean of 3	0.28	−0.07	**−0.47**	−0.401	−0.195	0.069	0.170	0.332	0.203

was −0.659 (*SE* 0.250) and was significant, and the lag-2 regression coefficient was −0.166 (*SE* 0.245) and was not significant. These values reflect the relatively short length of the time series (21 years versus recommended 25–30 years for time series analyses). If we accept this regression, these autoregressive estimates place the population in the cycle zone of Royama's (1992) periodicity diagram very close to the point of 6- to 7-year cycles. Hence, our populations show clear evidence of density dependence, but not of delayed density dependence.

Demographic responses.—Reproductive performance of *M. gapperi* was measured by mean number of lactating females (successful pregnancies) and mean number of recruits per year between periods of "high" numbers of voles (1997–1998, 2004–2005, 2011–2012) and periods of "low" numbers of voles (1995–1996, 1999–2003, 2006–2010, 2013–2015; Table 3). In terms of non-overlapping 95% *CI*s (Table 3), *M. gapperi* had more successful pregnancies, juvenile recruits, and adult recruits in high than low population years (Fig. 2). However, the mean index of early juvenile survival was 22% higher in low (2.36 ± 0.39) than high (1.84 ± 0.18) years of *M. gapperi* populations. This survival difference between low and high populations was 10% for juvenile males and 32% for juvenile females (Table 3; Fig. 3). In addition, there was a higher proportion of young-of-the-year voles breeding in the low years than high population years for both males (2.3 times) and females (1.9 times; Table 3). Mean J-S summer survival rates were similar when comparing these 2 periods of low and high abundance of *M. gapperi*, as were winter survival rates between the 2 levels of abundance (Table 3). However, mean monthly J-S summer survival was consistently lower than winter survival throughout the study (Fig. 4). Mean (± 95% *CI*) overall survival rates for the study were 0.58 ± 0.06 (summer, n = 21) and 0.83 ± 0.05 (winter, n = 19). In the years immediately prior to high populations, mean summer survival of *M. gapperi* increased from 0.46 to 0.64 (1997–1998), 0.53 to 0.64 (2004–2005), and 0.44 to 0.70 (2011–2012; Fig. 4). In all cases, these high populations declined during the following breeding season and subsequent winters (Fig. 1).

Coniferous seedfall.—In terms of amount of seed, there were 2 relatively heavy crops of interior spruce seed, in 1997 and 2013, with moderate to heavy crops in 2003 and 2009 (Fig. 5).

Table 2.—Autoregressive model parameter estimates from a 21-year time series for the 3 *Myodes gapperi* populations in British Columbia, Canada, and the combined mean population, following Bjørnstad et al. (1995). Fall population estimates were used unless otherwise noted. Statistically significant parameters are in bold. a_1 is a measure of direct density dependence, and a_2 is a measure of delayed density dependence.

Population	a_1	*SE* (a_1)	*P* (a_1)	a_2	*SE* (a_2)	*P* (a_2)	R^2
Grid Q	−0.62	0.34	0.10	−0.18	0.38	0.64	0.30
Grid S	**−0.72**	0.27	0.02	−0.32	0.28	0.27	0.49
Grid RZ	**−0.42**	0.18	0.03	−0.03	0.18	0.87	0.22
Mean of 3	**−0.93**	0.34	0.03	−0.50	0.64	0.45	0.50

Table 3.——Mean (*n* = 3 replicate sites) ± *SE* estimates of demographic responses of *Myodes gapperi* over 21 years in a coniferous forest landscape in British Columbia, Canada. High years include 1997–1998, 2004–2005, 2011–2012; low years include 1995–1996, 1999–2003, 2006–2010, 2013–2015. J-S = Jolly-Seber.

Parameter	High years	Low years	Overall
Successful pregnancies[a]	15.9 ± 2.6	6.8 ± 0.8	9.4 ± 1.3
Total recruits[a]	42.7 ± 5.0	20.3 ± 1.9	26.7 ± 3.0
Juvenile recruits[a]	25.8 ± 2.9	11.4 ± 1.1	15.5 ± 1.8
Juvenile survival	1.84 ± 0.18	2.36 ± 0.39	2.21 ± 0.28
Males	1.02 ± 0.14	1.13 ± 0.19	1.10 ± 0.14
Females	0.84 ± 0.06	1.23 ± 0.21	1.12 ± 0.15
Young-of-the-year breeding			
Males	0.15 ± 0.03	0.35 ± 0.08	0.23 ± 0.01
Females	0.34 ± 0.07	0.65 ± 0.11	0.50 ± 0.07
Summer J-S survival	0.60 ± 0.03	0.57 ± 0.02	0.58 ± 0.02
Winter J-S survival	0.82 ± 0.01	0.84 ± 0.02	0.83 ± 0.01
Number of years	*n* = 6	*n* = 15	*n* = 21

[a] Non-overlapping 95% *CI*s between high and low years.

Subalpine fir also had 2 heavy crops, in 2002 and 2009, with 3 moderate crops in 1997, 2000, and 2003 (Fig. 5). The 2 concurrent seed crops in the fall of 1997 occurred when mean abundance of *M. gapperi* was already increasing during summer months, but may have contributed to high vole numbers in September and October of that year, and relatively high numbers (19.4) in May 1998 (Fig. 1). Although a breeding season decline occurred in early summer 1998, *M. gapperi* mean abundance did rebound to 19.5 animals, possibly owing to the substantial seed supply that enhanced reproduction. The next seedfall events in 2000 and 2002 (subalpine fir) and 2003 (both species) preceded, and may have contributed to, the high numbers of *M. gapperi* in 2004–2005. Similarly, both tree species had cone crops in 2009, but again more than 1 year prior to high numbers of *M. gapperi* (Fig. 5). The final seed crops of spruce and subalpine fir in 2013 occurred after the last period of high abundance in 2011–2012 and did not lead to a population increase in *M. gapperi* (Fig. 5). Cone crops of Douglas-fir were ranked as good, medium, and poor on a relative basis. Good crops appeared to occur in 1995, 2009, 2012, and 2013 and may have contributed to increased numbers of *M. gapperi*. Lodgepole pine seed rain from MPB-killed trees may have occurred after 2008, but we have no seed collection data.

DISCUSSION

Populations of *M. gapperi* showed fluctuations in density with approximately 7 years between high numbers over a 21-year period in old-growth mixed coniferous forest. This characterization of our *M. gapperi* populations aligned with the majority of red-backed vole population studies in North America where classical 3- to 4-year cycling was uncommon (Boonstra and Krebs 2012). Density (maximums of 25 to 32 and minimums < 5 voles/ha) and pattern of population change (irregular fluctuations) fit those reported by Boonstra and Krebs (2012) for the data collected by Merritt et al. (2001). Grant (1976), from an 11-year study, reported 2 peaks in abundance of *M. gapperi* at a 10-year interval in southern Quebec, and Fuller (1977), from a 15-year study, showed 2 peaks 2 years apart in the Northwest Territories. Our *M. gapperi* data are the longest recorded population study with multiple sampling sessions each year. Measurements of vole reproduction, recruitment, and survival indicated that temporary breeding season declines were common, overall summer survival of voles was poorer than winter survival, and early juvenile survival of voles was consistently poor throughout the study. The strength of our analysis was in the time series of data as spatial replication (*n* = 3) was minimal.

Evaluation of the food supply hypotheses.—Our H_1 that increased food supplies from fall masting of spruce and subalpine fir would enhance overwinter survival of *M. gapperi*, as well as enhance reproductive output in the summer breeding period following the masting event, was partially supported for 3 of 4 seedfall events. However, there are 3 important caveats to this conclusion. First, the spruce and subalpine fir seedfall data were collected from the Sicamous long-term study area. Douglas-fir seedfall data were collected from a variety of locations in relatively undisturbed forests in the Okanagan-Thompson region. We have inferred that these same moderate and heavy seedfall events also occurred in our study area. This assumption seemed reasonable considering the wide geographical area over which northern coniferous cone crops are synchronous (Koenig and Knops 1998), and is verified by cone crop survey data.

Second, the effects of a substantial seed supply seemed to enhance reproduction and survival in the fall of the seed year, and in the summer and fall of the year after the seedfall event. In addition, there seemed to be a carry-over effect into a 2nd year after the actual seedfall event, as indicated in 2004–2005 and 2011–2012. Alternatively, if seed supplies on the forest floor were exhausted in the winter and spring-summer after the seedfall event, then some other factor was responsible for increasing vole populations. Caching of coniferous seeds by rodents is common (Abbot and Quink 1970; Vander Wall 1990) and may have extended the period of relative food abundance. Similarly, Lobo and Millar (2013) hypothesized that invertebrates associated with subalpine fir seeds may provide a secondary food source for voles, to offset the inhibition of feeding on these seeds by *M. gapperi* (Lobo and Millar 2011). This apparent multi-year delay in response to fluctuating food resources has also been recorded for avian predators and emergence of periodical cicadas (*Magicicada* spp.—Koenig and Liebhold 2005).

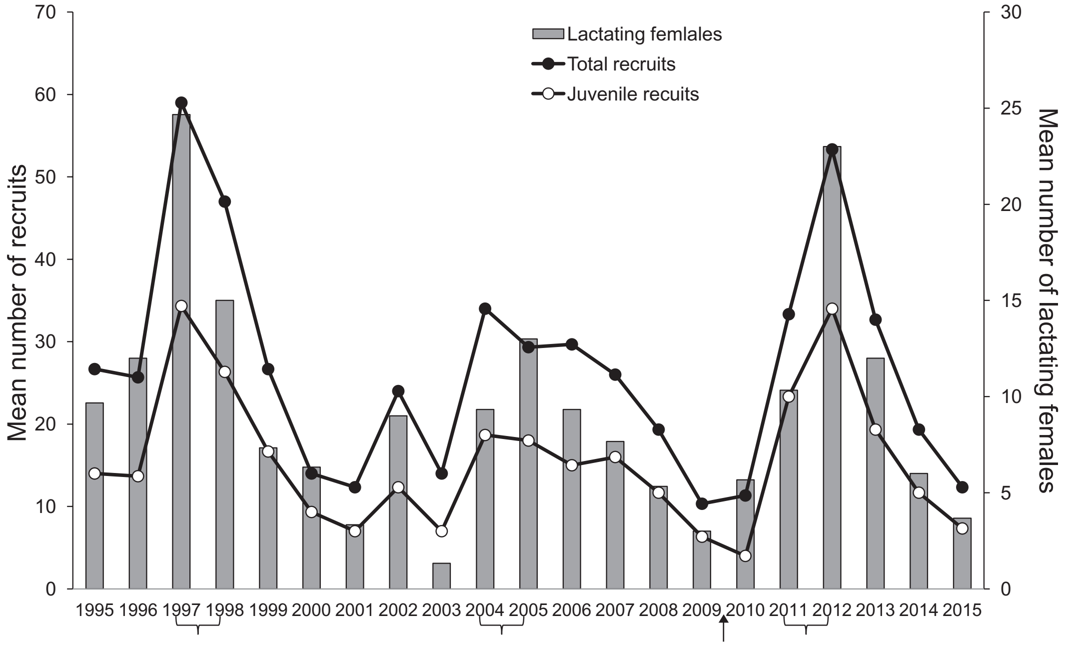

Fig. 2.—Mean ($n = 3$ replicate sites) number of juvenile and total recruits and number of lactating females (successful pregnancies) of *Myodes gapperi*, 1995 to 2015, in old-growth forest in southern British Columbia, Canada. Years of "high" abundance are indicated along x-axis. Arrow indicates year of grid replacement.

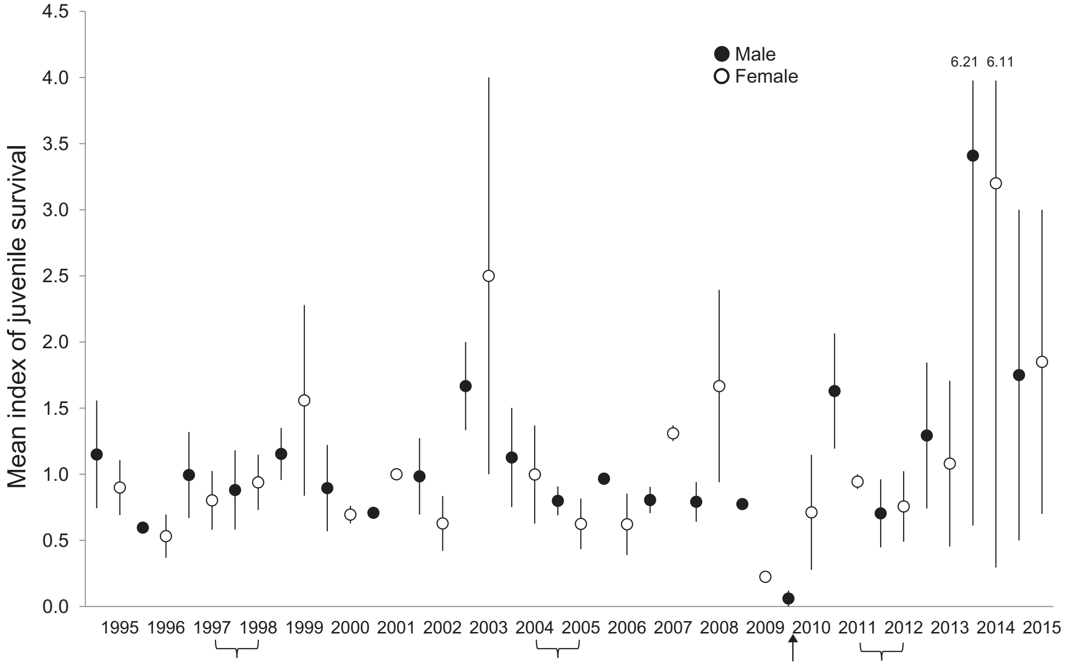

Fig. 3.—Mean ($n = 3$ replicate sites ± *SE*) index of early juvenile survival for male and female *Myodes gapperi*, 1995 to 2015, in old-growth forest in southern British Columbia, Canada. Years of "high" abundance are indicated along x-axis. Arrow indicates year of grid replacement.

We assumed that *M. gapperi* would consume Douglas-fir seed but could not find a reference for this in the literature.

Third, red squirrels (*Tamiasciurus hudsonicus*) are a major seed predator of conifer seeds and likely competed with *M. gapperi* (Steele 1998). The 2006–2008 period had minimal seedfall and mean ($n = 3$ trapping grids) numbers of squirrels ranged between 1–2/ha (Sullivan et al. 2010). Similarly, mean ($n = 3$) numbers of red squirrels in 2014–2015 after a substantial seedfall event in 2013 were at this same level of 1–2/ha (T. P. Sullivan and D. S. Sullivan, pers. obs.). Hence, red squirrel population fluctuations did not occur and thus it was unlikely that they dampened vole population changes.

We have no explanation for the lack of response (declining numbers) of *M. gapperi* after the major seedfall in 2013.

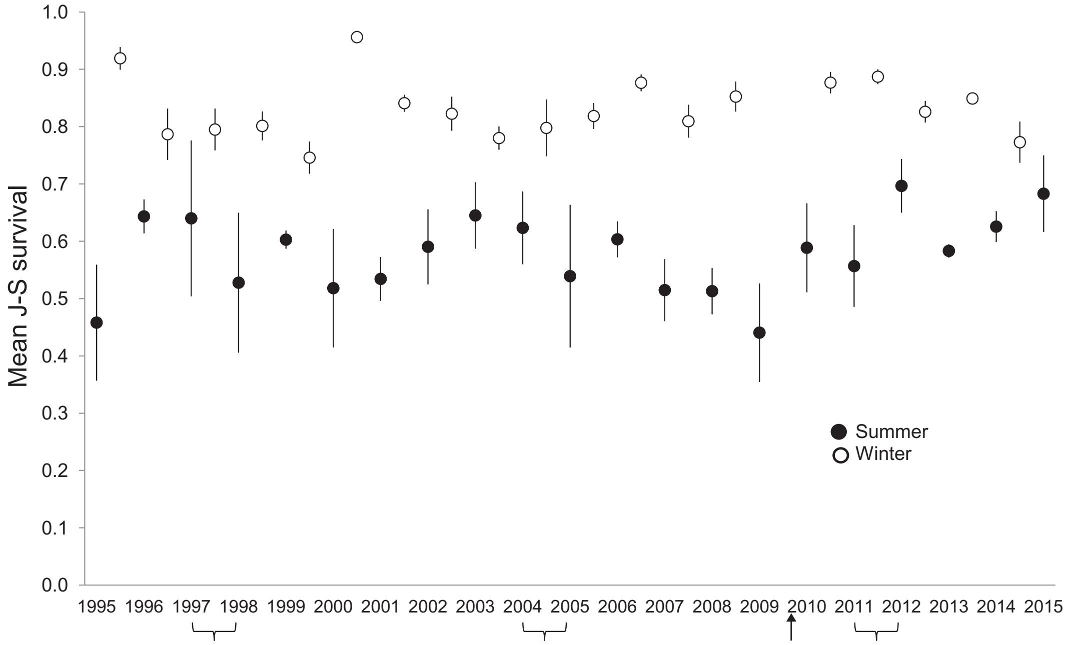

Fig. 4.—Mean (*n* = 3 replicate sites ± *SE*) Jolly-Seber survival of *Myodes gapperi* as seasonal summer and winter periods each year, 1995 to 2015, in old-growth forest in southern British Columbia, Canada. Years of "high" abundance are indicated along x-axis. Arrow indicates year of grid replacement.

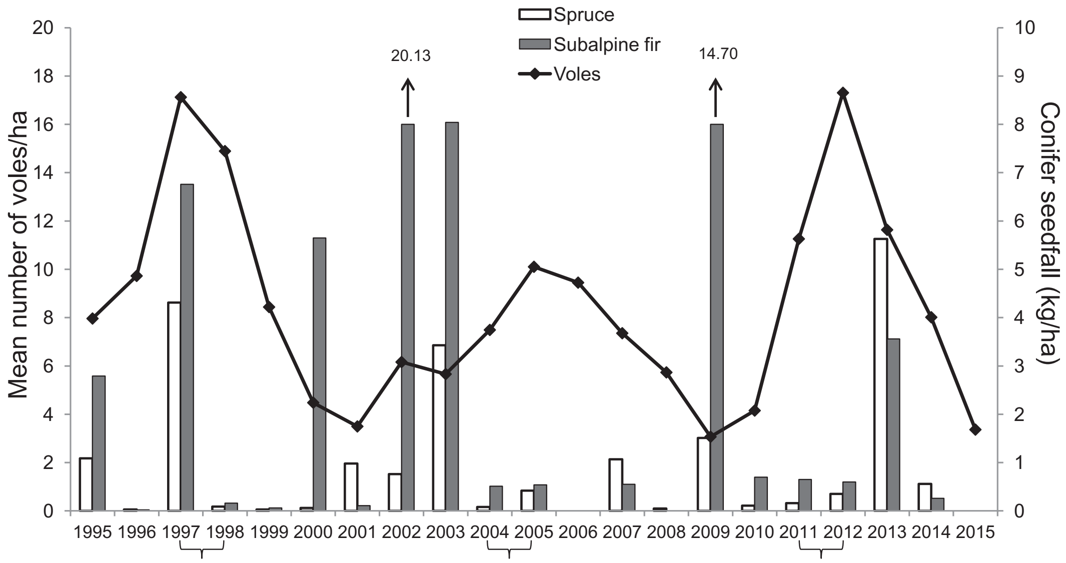

Fig. 5.—Mean number of *Myodes gapperi* per ha as an index during summer periods each year and seedfall (kg/ha) of spruce and subalpine fir during 1995 to 2015 in old-growth forest in southern British Columbia, Canada. Seedfall mass for a given year was for the seedfall event in that year.

However, Elias et al. (2006) related seed production from white pine with peaks in masting preceding 4 of 5 peaks in *M. gapperi*. In at least 1 seedfall event (1984), numbers of *M. gapperi* continued to increase in a 2nd year after the event, whereas in a moderate seedfall year (1990), numbers of voles declined (Fig. 3; Elias et al. 2006). Thus, seedfall events may not always lead to population increases in *M. gapperi*. Indeed, Boonstra and Krebs (2006) found no correlation between white spruce seed crops and population changes in *M. rutilus* in the Yukon.

H_2 is that the potentially increased food supply from "seed rain" by dead, standing lodgepole pine and the accumulation of fallen pine trunk and branch debris for cover would enhance habitat conditions for *M. gapperi* and support the high numbers of voles in 2011–2012. An interesting ecological process of seed dispersal seems to follow in MPB-killed lodgepole pine stands where a "seed rain" occurs over at least 9 years after an MPB outbreak (Teste et al. 2011). In live stands, lodgepole pine is primarily a serotinous species, awaiting wildfire to break resin seals on cone scales to release seeds (Lotan and Perry 1983). However, this process is circumvented by tree death whereby lodgepole pine seed is dispersed widely via canopy-cone opening on trees or locally via fallen ground-cone opening during the years after trees die from MPB (Teste et al. 2011). This potentially sustained "pine seed rain" may have enhanced populations of ground-foraging vertebrates such as *M. gapperi* and other seed-eating species. In both laboratory and field experiments, this vole readily eats lodgepole pine seed and secondarily eats white spruce seed (Lobo et al. 2009). Lodgepole pine seeds seem to remain viable in cones on trees and on the ground during the years after MPB attack (Teste et al. 2011). Thus, in lodgepole pine stands with some MPB-killed trees, there was a 4th potential source of conifer seed, along with fluctuations of Douglas-fir, interior spruce, and subalpine fir cone crops that occurred in our general study area.

Responses in abundance of *M. gapperi* populations to MPB-killed stands in western North America have ranged from a moderate positive effect in Utah (Stone 1995), to an intermediate effect as indicated by increased abundance between clear-cuts and live old-growth forest in central BC (D. B. Ransome and T. P. Sullivan, pers. obs.), to no effect in Wyoming (Saab et al. 2014). These results contrast with an inverse relationship between abundance (but not survival) of the northern red-backed vole (*M. rutilus*) and the level of spruce mortality from spruce beetle (*D. rufipennis*) in Alaska (McDonough and Rexstad 2005).

Another aspect of MPB-killed trees in lodgepole pine stands is an accumulation of fallen woody debris (branches and trunks) on the forest floor 5–10 years after MPB attack that may generate positive responses for forest-floor small mammals in the post-epidemic period (Klutsch et al. 2009; Saab et al. 2014). However, we know of no studies that have measured debris accumulations in dead lodgepole pine forests and related these metrics to small mammal abundance. Compared with a dispersed (conventional) treatment on clear-cut sites, constructed habitats of post-harvest woody debris arranged in large piles and windrows enhanced the abundance and demography of *M. gapperi* for at least 3 years post-harvest (Sullivan et al. 2011). Pauli et al. (2006) and Fauteux et al. (2012) reported similar positive effects on abundance of *M. gapperi* in sites of extensive blowdown of mature coniferous forest and on those sites with high volumes of coarse woody debris, respectively. Thus, *M. gapperi* populations appear to benefit from increased woody debris accumulations that provide a suitable moist microclimate, sufficient cover, and likely fungal sporocarps in decayed wood, seeds, and saproxylic invertebrates (Jacobs and Work 2012) as food sources. Fruiting bodies of hypogeous fungi seem to be in greater abundance in woody debris than soil (Amaranthus et al. 1994).

Although berry-producing shrubs such as *A. uva-ursi*, *Vaccinium* spp., *Empetrum nigrum*, and *Shepherdia canadensis* were of low abundance or lacking in our study areas owing to the relatively dense forest cover, their berries have been reported as important to *M. rutilus*, potentially driving population fluctuations (Dyke 1971; Krebs et al. 2010). Thus, in our area, fluctuations in dwarf-shrub berry crops were not the driver of population change. In experimental berry additions in 2 summers, Dracup et al. (2016) reported that short-term pulses of fruit had no effect on demography of *M. gapperi* populations.

The delays in response of *M. gapperi* populations to heavy seed crops and potentially ambiguous response to subalpine fir seed are problematic. This microtine requires closed-canopy forest and disappears on clear-cuts, often within a year after harvest, at least in western North America (Fisher and Wilkinson 2005; Zwolak 2009). Recovery of *M. gapperi* in 2nd-growth forest to abundance levels found in late successional forests takes many decades (Sullivan et al. 2010). Several other studies from western North America also reported that abundance of *M. gapperi* declined on clear-cuts (Gashwiler 1970; Martell 1983; Sullivan et al.1999; Sullivan and Sullivan 2001; Klenner and Sullivan 2003). In contrast, Kirkland (1990) reviewed 21 published studies and concluded that *M. gapperi* was principally responsible for the greater abundance of microtine rodents on recent clear-cuts, increasing in abundance in 15 of 21 studies. This contradiction may relate to differences in diet of *M. gapperi* in eastern North America where forest clearing for agriculture and wood products has occurred for at least 300 years. *M. gapperi* may have adapted to conditions in eastern forests whereby fungi and lichens have been substituted in their diet by other items such as seeds, leaves, and berries (Schloyer 1977; Gliwicz and Glowacka 2000). Alternatively, this species and other northern rodents having large geographic ranges may have ecotypic differences in diet across their entire range, and thus a uniform response to environmental change and food is unlikely. Hence, the species may have evolved a much more diverse diet and flexibility in food selection than previously thought (Soininen et al. 2013).

Evaluation of the social interaction hypothesis.—H_3 predicted that spring reorganization via poor survival of juvenile voles would lead to breeding season declines in abundance of *M. gapperi*. At least some level of decline occurred in 17 of 21 years and reflected the generally poor overall summer survival, which seemed to be related to early juvenile survival of both male and female voles that was consistently low. The overall mean of 2.21 juvenile animals per lactating female was 43% of the expected numbers based on a mean litter size in BC of 4.9 (range 2–8—Nagorsen 2005). Thus, H_3 was partly supported for a reorganization event that led to breeding season declines, and the cause may have been poor survival of juvenile voles. In peak population years, a transient spring decline in numbers clearly did not lead to an overall breeding season decline. Summer breeding season declines might be related to predator-induced maternal stress impacting reproduction and survival of voles, as reported for snowshoe hares (*Lepus americanus*—Sheriff et al. 2015). However, the evidence indicates that voles do not respond with predator-induced reproductive suppression (see Boonstra 2013 for a review), so we think this is not the explanation.

As reviewed by Boonstra and Krebs (2012), *Myodes* in North America have the behavioral organization in which spacing behavior (e.g., spring reorganization) can potentially limit the number of breeding animals by density-dependent inhibition of maturation of juveniles. Our higher proportion of young-of-the-year voles breeding (both males and females) in the low years than high years supported this premise, as was also reported for *M. rutilus* by Gilbert et al. (1986). If this process occurs, as in Fennoscandian *Myodes*, population cycling can happen (Oli and Dobson 1999, 2001). Population cycles are potentially absent if this inhibition process does not occur (Boonstra 1994; Oli and Dobson 2001).

Predation risk by small weasels.—Fennoscandian studies have suggested that predators cause population declines in various microtine species (Henttonen et al. 1987; Hanski et al. 1991) with both numerical and functional responses of small weasels to prey abundance (Korpimaki et al. 1991). In eastern Canada, Johnson et al. (2000) suggested that *M. erminea* populations showed cyclic dynamics that may have been related to potentially cycling prey species such as *M. gapperi*. Conversely, Boonstra and Krebs (2006) concluded that weasel predation on *M. rutilus* in the Yukon was irrelevant if densities of voles were chronically low, resulting in chronically low weasel densities. Cheveau et al. (2004) concluded that the irruptions of the boreal owl (*Aegolius funereus*) depended on the presence of abundant and cyclic populations of small mammals such as *M. gapperi* (Fauteux et al. 2015). However, Boonstra and Krebs (2012) concluded that changes in the density of specialist owls were not caused by changes in populations of *M. gapperi*. Our densities of *M. gapperi* were presumably high enough to sustain weasel populations through time.

Based on our results, tentative conclusions about changes in our *M. gapperi* populations were that they had 1) regular fluctuations related to pulsed food supplies in the form of coniferous seeds; 2) clear and consistent breeding season declines, typical of Fennoscandian *Myodes* populations that cycle; 3) poor juvenile survival of both males and females, particularly at high densities; and 4) early breeding season declines that presumably result from density-dependent social inhibition and, potentially, can be one cause of a population cycle. Additionally, poor summer survival could be due to the presence of weasels, a hypothesis that remains to be tested in our system.

As outlined by Boonstra and Krebs (2012), we need rigorous, large-scale, year-round field experiments testing the overwinter food, spring reorganization, and weasel predation hypotheses as mechanisms driving population change in this keystone species. *M. gapperi* may be a logical species to test these predictions experimentally, since it has breeding season declines and seems to feed on some species of conifer seeds, at least in coniferous forests of western North America. Food supplementation experiments need to investigate both "pulsed" and "continuous" feeding regimes to determine the carry-over effect of food supplies (e.g., conifer seeds) as suspected in this study. Weasel removal experiments similar to those of Graham and Lambin (2002) would help disentangle the relative importance of predators for these populations of *M. gapperi*.

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Literature Cited

Abbot, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51:271–278.

Alexander, R. R., R. C. Shearer, and W. D. Shepperd. 1990. *Abies lasiocarpa* (Hook.) Nutt. Subalpine Fir. Pp. 60–70 in Silvics of North America. Volume 1. Conifers (R. M. Burns and B. H. Honkala, Technical Coords.). United States Department of Agriculture, Forest Service, Agriculture Handbook 654.

Alexander, R. R., and W. D. Shepperd. 1990. *Picea engelmannii* Parry ex Englem. Engelmann spruce. Pp. 187–203 in Silvics of North America. Volume 1. Conifers (R. M. Burns and B. H. Honkala, Technical Coords.). United States Department of Agriculture, Forest Service, Agriculture Handbook 654.

Amaranthus, M., J. M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24:2157–2165.

Bjørnstad, O. N., W. Falck, and N. C. Stenseth. 1995. A geographic gradient in small rodent density fluctuations: a statistical modeling approach. Proceedings of the Royal Society of London, B. Biological Sciences 262:127–133.

Boonstra, R. 1994. Population cycles in microtines: the senescence hypothesis. Evolutionary Ecology 8:196–219.

Boonstra, R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Functional Ecology 27:11–23.

Boonstra, R., and C. J. Krebs. 2006. Population limitation of the northern red-backed vole in the boreal forests of northern Canada. Journal of Animal Ecology 75:1269–1284.

Boonstra, R., and C. J. Krebs. 2012. Population dynamics of red-backed voles (*Myodes*) in North America. Oecologia 168: 601–620.

Cheveau, M., P. Drapeau, L. Imbeau, and Y. Bergeron. 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. Oikos 107:190–198.

Dracup, E. C., D. M. Keppie, and G. J. Forbes. 2016. The short-term impact of abundant fruit upon deer mouse (*Peromyscus maniculatus*), southern red-backed vole (*Myodes gapperi*), and woodland jumping mouse (*Napaeozapus insignis*) populations. Canadian Journal of Zoology 94:555–563.

Dyke, G. R. 1971. Food and cover of fluctuating populations of northern cricetid rodents. Ph.D. dissertation, Department of Zoology, University of Alberta, Edmonton, Alberta, Canada.

Elias, S. P., J. W. Witham, and M. L. Hunter. 2006. A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in Maine. Journal of Mammalogy 87:440–445.

Fauteux, D., M. Cheveau, L. Imbeau, and P. Drapeau. 2015. Cyclic dynamics of a boreal southern red-backed vole population in northwestern Quebec. Journal of Mammalogy 96:1–6.

Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest Ecology and Management 266:194–205.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammalian Reviews 35:51–81.

Fuller, W. A. 1977. Demography of a subarctic population of *Clethrionomys gapperi*: numbers and survival. Canadian Journal of Zoology 55:42–51.

Gashwiler, J. S. 1970. Plant and mammal changes in a clearcut in west-central Oregon. Ecology 51:1018–1026.

Gilbert, B. S., C. J. Krebs, D. Talarico, and D. B. Cichowski. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? Journal of Animal Ecology 55:543–552.

Gliwicz, J., and B. Glowacka. 2000. Differential responses of *Clethrionomys* species to forest disturbance in Europe and North America. Canadian Journal of Zoology 78:1340–1348.

Graham, I. M., and X. Lambin. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. Journal of Animal Ecology 71:946–956.

Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. Canadian Journal of Zoology 54:2156–2173.

Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57:32–44.

Hansen, T. F., N. C. Stenseth, and H. Henttonen. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. American Naturalist 154:129–139.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60:353–367.

Henttonen, H., T. Oksanen, A. Jortikka, and V. Haukisalmi. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? Oikos 50:353–365.

Hermann, R. K., and D. P. Lavender. 1990. *Pseudotsuga menziesii* (Mirb.) Franco. Douglas fir. Pp. 60–70 in Silvics of North America. Volume 1. Conifers (R. M. Burns and B. H. Honkala, Technical Coords.). United States Department of Agriculture, Forest Service, Agriculture Handbook 654.

Jacobs, J. M., and T. T. Work. 2012. Linking deadwood-associated beetles and fungi with wood decomposition rates in managed black spruce forests. Canadian Journal of Forest Research 42:1477–1490.

Johnson, D. R., B. J. Swanson, and J. L. Eger. 2000. Cyclic dynamics of eastern Canadian ermine populations. Canadian Journal of Zoology 78:835–839.

Kirkland, G. L. 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos 59:313–320.

Klenner, W., and T. P. Sullivan. 2003. Partial and clear-cut harvesting of high-elevation spruce-fir forests: implications for small mammal communities. Canadian Journal of Forest Research 33:2282–2296.

Klutsch, J. G., et al. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. Forest Ecology and Management 258:641–649.

Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. Nature 396:225–226.

Koenig, W. D., and J. M. H. Knops. 2005. The mystery of masting in trees. American Scientist 93:340–347.

Koenig, W. D., and A. M. Liebhold. 2005. Effects of periodical cicada emergences on abundance and synchrony of avian populations. Ecology 86:1873–1882.

Korpimaki, E., K. Norrdahl, O. Huitu, and T. Klemola. 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. Proceedings of the Royal Society of London, B. Biological Sciences 272:193–202.

Korpimaki, E., K. Norrdahl, and T. Rinta-Jaskari. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? Oecologia 88:552–561.

Krebs, C. J. 1999. Ecological methodology. Addison Wesley Longman, Inc., Menlo Park, California.

Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.

Krebs C. J., and R. Boonstra. 1978. Demography of the spring decline in populations of the vole *Microtus townsendii*. Journal of Animal Ecology 47:1007–1015.

Krebs, C. J., and R. Boonstra. 1984. Trappability estimates for mark-recapture data. Canadian Journal of Zoology 62:2440–2444.

Krebs, C. J., R. Boonstra, S. Gilbert, D. Reid, A. J. Kenney, and E. J. Hofer. 2011. Density estimation for small mammals from live-trapping grids: rodents in northern Canada. Journal of Mammalogy 92:974–981.

Krebs, C. J., K. Cowcil, R. Boonstra, and A. J. Kenney. 2010. Do changes in berry crops drive population fluctuations of rodents in the southwestern Yukon? Journal of Mammalogy 91:500–509.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587–607.

Leadem, C. L., S. L. Gillies, H. K. Yearsley, V. Sit, D. L. Spittlehouse, and P. J. Burton. 1997. Field studies of seed biology. Land management handbook 40. B.C. Ministry of Forests Research Program.

Lobo, N., M. Duong, and J. S. Millar. 2009. Conifer-seed preferences of small mammals. Canadian Journal of Zoology 87:773–780.

Lobo, N., and J. S. Millar. 2011. The efficacy of conifer seeds as major food resources to deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). Mammalian Biology 76:274–284.

Lobo, N., and J. S. Millar. 2013. Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. Journal of Animal Ecology 82:814–825.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. Agriculture Handbook 606. USDA, Washington, D.C.

Lloyd, D. A., K. Angove, G. Hope, and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Manage. Handb. 23.

Martell, A. M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Canadian Field-Naturalist 95:325–328.

Martell, A. M. 1983. Demography of southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) after logging in north-central Ontario. Canadian Journal of Zoology 61:958–969.

Maser, C., A. W. Claridge, and J. M. Trappe. 2008. Trees, truffles, and beasts: how forests function. Rutgers University Press, Piscataway, New Jersey.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal inter-relationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.

McDonough, T. J., and E. Rexstad. 2005. Short-term demographic response of the red-backed vole to spruce beetle infestations in Alaska. Journal of Wildlife Management 69:246–254.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series No. 6. Research Branch Ministry of Forests, Victoria, British Columbia, Canada.

Merritt, J. F. 1981. *Clethrionomys gapperi.* Mammalian Species No. 146. American Society of Mammalogists, Provo, Utah.

Merritt, J. F., M. Lima, and F. Bozinovic. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94:505–514.

Merritt, J. F., and J. M. Merritt. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. Journal of Mammalogy 59:576–598.

Nagorsen, D. W. 2005. Rodents and lagomorphs of British Columbia. Royal BC Museum, Victoria, Canada.

Nienstaedt, H., and J. C. Zasada. 1990. *Picea glauca* (Moench) Voss. White spruce. Pp. 204–226 in Silvics of North America. Volume 1. Conifers (R. M. Burns and B. H. Honkala, Technical Coords.). United States Department of Agriculture, Forest Service, Agriculture Handbook 654.

Nordyke, K. A., and S. W. Buskirk. 1991. Southern red-backed vole, *Clethrionomys gapperi,* populations in relation to stand succession and old-growth character in the central Rocky mountains. Canadian Field-Naturalist 105:330–334.

Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of sexual maturity. Oikos 86:557–568.

Oli, M. K., and F. S. Dobson. 2001. Population cycles in small mammals: the alpha-hypothesis. Journal of Mammalogy 82: 573–581.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

Ovaska, K., and T. H. Herman. 1986. Fungal consumption by six species of small mammals in Nova Scotia. Journal of Mammalogy 67:208–211.

Parish, R., J. A. Antos, and M.-J. Fortin. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. Canadian Journal Forest Research 29:1347–1356.

Pauli, J. N., B. E. Bedrosian, and N. Osterberg. 2006. Effects of blowdown on small mammal populations. American Midland Naturalist 156:151–162.

Pearce, J., and L. Venier. 2005. Small mammals as bioindicators of sustainable boreal forest management. Forest Ecology and Management 208:153–175.

Raphael, M. G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. Pp. 359–367 in Management of amphibians, reptiles, and small mammals in North America (R. C. Szaro, K. E. Severson, and D. R. Patton, Technical eds.). USDA Forest Service General Technical Report RM-166.

Royama, T. 1992. Analytical population dynamics. Chapman and Hall, London, United Kingdom.

Saab, V. A., et al. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60:539–559.

Safranyik, L., and B. Wilson. 2006. The mountain pine beetle. A synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Victoria, British Columbia, Canada.

Schloyer, C. R. 1977. Food habits of *Clethrionomys gapperi* on clearcuts in west Virginia. Journal of Mammalogy 58:677–678.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin and Co. Ltd., London, England.

Sheriff, M. J., E. McMahon, C. J. Krebs, and R. Boonstra. 2015. Predator-induced maternal stress and population demography in snowshoe hares: the more severe the risk, the longer the generational effect. Journal of Zoology 296:305–310.

Sikes, R. S., W. L. Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Soininen, E. M., V. T. Ravolainen, K. A. Brathen, N. G. Yoccoz, L. Gielly, and R. A. Ims. 2013. Arctic small rodents have diverse diets and flexible food selection. PLoS One 8:e68128.

Statistica. 2013. Dell Software, Round Rock, Texas.

Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species No. 586:9.

Stone, W. E. 1995. The impact of a mountain pine beetle epidemic on wildlife habitat and communities in post-epidemic stands of a lodgepole pine forest in northern Utah. Ph.D. dissertation, Utah State University, Logan.

Sullivan, T. P., R. A. Lautenschlager, and R. G. Wagner. 1999. Clear-cutting and burning of northern spruce-fir forests: implications for small mammal communities. Journal of Applied Ecology 36:327–344.

Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology 38:1234–1252.

Sullivan, T. P., D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome. 2010. Green-tree retention and life after the beetle: stand structure and small mammals 30 years after salvage harvesting. Silva Fennica 44:749–774.

Sullivan, T. P., D. S. Sullivan, P. M. F. Lindgren, D. B. Ransome, J. G. Bull, and C. Ristea. 2011. Bioenergy or biodiversity: woody debris structures and maintenance of red-backed voles on clearcuts. Biomass and Bioenergy 35:4390–4398.

Teste, F. P., V. J. Liefers, and S. M. Landhäusser. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecological Applications 21:150–162.

Thompson, I. D., and P. Angelstam. 1999. Special species. Pp. 434–459 in Maintaining biodiversity in forest ecosystems (M. L. Hunter, ed.). Cambridge University Press, Cambridge, United Kingdom.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, New Jersey.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois.

Viereck, L. A., and W. F. Johnston. 1990. *Picea mariana* (Mill.) B.S.P. Black Spruce. Pp. 227–237 in Silvics of North America. Volume 1. Conifers (R. M. Burns and B. H. Honkala, Technical Coords.). United States Department of Agriculture, Forest Service, Agriculture Handbook 654.

Walton, A., et al. 2009. Provincial-level projection of the current mountain pine beetle outbreak. British Columbia Ministry of Forests and Range, Victoria, British Columbia, Canada.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Zwolak, R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecology and Management 258:539–545.

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