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Population regulation in the deer mouse (*Peromyscus maniculatus*) in old-growth coniferous forests of southern British Columbia: insights from a long-term study

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Abstract

We report a 26-year detailed record of changes in abundance and demography of the deer mouse (*Peromyscus maniculatus*) in old-growth coniferous forest in southern British Columbia, Canada, from 1995 to 2020. We evaluated three separate hypotheses that may help to explain population changes: (H_1) large cone crops of coniferous trees will correspond to peak *Peromyscus* density; (H_2) spring reorganization of individuals within populations will lead to early breeding season declines; and (H_3) competition between *P. maniculatus* and the sympatric red-backed vole (*Clethrionomys gapperi*) and hence densities of the former will be lower when the latter are higher. Populations of deer mice showed five periods of high numbers with intervals of 3 to 8 years between fluctuations. Mean density ranges were low, growing from 2–3/ha in spring to 8–13/ha in autumn. The mean abundance of *P. maniculatus* in high years was directly related to number of successful pregnancies, total number of juvenile recruits, and a high index of early juvenile productivity. Irregular population fluctuations were related to pulsed food supplies in the form of coniferous seeds, thereby supporting H_1. Numbers declined in 16 of 26 summers, reflecting poor overall survival and low reproduction (only 69% of adult females lactating and 51% having only one litter; virtually no juveniles matured and bred). Thus, H_2 was partly supported for a reorganization event that led to breeding season declines, and the immediate cause was very poor survival of juvenile mice. The annual peak numbers of *C. gapperi* ranged from 1.5 to 16.9 times higher than numbers for *P. maniculatus* and hence provided only weak support for H_3. Field experiments are needed to test these hypotheses as mechanisms driving deer mouse populations.

Keywords Cone crops · Coniferous forest · Demographic changes · *Peromyscus maniculatus* · Population regulation · Spring reorganization

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Introduction

One of the central questions of population ecology is that of population regulation—what prevents a population from growing to infinity or declining to extinction. Theory states that density-dependent processes must operate to bring a growing population back to equilibrium density and thus stability (Sinclair 1989; Krebs 2002). These processes range from extrinsic factors (food limitation, predation, disease, climate) to intrinsic ones (social behavior, dispersal, physiological mechanisms, alternating epigenetic phenotypes) and their interactions. In addition, given the rapidity and impact of climate change, it is critical to understand the population processes driving demography and the capacity of species to adapt. Here, we use a long-term observational study to understand the population regulatory mechanisms driving

the widest distributed small mammal in North America—the deer mouse (*Peromyscus maniculatus*).

The deer mouse occupies a broad range of forested, shrub-steppe, grassland, and rocky alpine habitats across much of North America from the Mexican plateau to the tree line in northern Canada (Baker 1968; Naughton 2012). The white-footed mouse (*P. leucopus*) is sympatric with *P. maniculatus* in the Midwest and Northeastern United States (US) occupying broadleaved forests and shrub-dominated fields (Lackey et al. 1985). *Peromyscus* populations generally show a seasonal change in abundance with low spring breeding densities and high densities through the fall and winter with generally similar patterns of abundance from 1 year to the next (e.g., Terman 1968; Grant 1976; Merritt et al. 2001). *Peromyscus* feed on a wide range of plant and plant products including seeds from coniferous and broadleaved trees, fungi, berries, and arthropods (Jameson 1952; Maser et al. 1978; Bellocq and Smith 1994; Lobo et al. 2009).

Multi-annual population patterns vary widely across North America. There was little interannual variability in abundance of *P. maniculatus* in long-term studies in the Yukon territory (17 years) (Gilbert and Krebs 1991) and southwestern Alberta (16 years), Canada (Millar and McAdam 2001). In contrast, there was considerable variability among years in a 43-year study in Ontario (Fryxell et al. 1998) and in a 20-year study in Pennsylvania (Merritt et al. 2001) but neither found cyclic fluctuations in abundance. In these two studies, numbers were not constant over time, but there was no mathematical pattern to their fluctuations. Similarly, Lewellyn and Vessey (1998) reported little evidence for interannual cycles in *P. leucopus* in Ohio. However, in other long-term (10 to 36 years) studies, some *Peromyscus* populations do seem to have multi-annual fluctuations in abundance associated with coniferous seed or broadleaved mast crops. Examples include abundance of *P. maniculatus* linked to Douglas-fir (*Pseudotsuga menziesii*) seed in Oregon (Gashwiler 1965, 1979) to white spruce (*Picea glauca*) seed in the southern Alberta foothills (Lobo and Millar 2013) and to sugar maple (*Acer saccharum*) crops in Ontario (Falls et al. 2007). Similarly, *P. leucopus* populations are linked to acorn (*Quercus*) crops in Virginia (Wolff 1996) and to acorn and red maple (*A. rubrum*) crops in Maine (McCracken et al. 1999; Elias et al. 2004).

In all these studies, there were some seasons or years when *Peromyscus* populations either did not increase or declined in spite of substantial seed or mast crops, and this demonstrates that mast crops are not sufficient by themselves to drive dynamics (McShea 2000; Elias et al. 2004). An analysis by Millar and McAdam (2001) identified nestling survival as the key driver, and this early survival was not related to food, but possibly weather. Similarly, inconsistent results in studies with supplemental food and *Peromyscus* included population declines and low reproduction in summer (Terman 1999; Vessey 1987) or apparent limited responses in abundance as reviewed by Dracup et al. (2016). Thus, changes in food abundance (e.g., seed crops) may not be a necessary or sufficient cause for deer mouse populations to increase.

Although Wolff (1997) concluded that intrinsic factors were not likely to regulate populations of *Peromyscus*, the inconsistent population responses to natural and supplemental food studies suggest otherwise. Extra food (natural or supplemental) causes an increased population abundance of *Peromyscus* but seemingly only at low or moderate densities, at least with respect to very large seed and mast crops. Other factors such as territorial spring reorganization and inhibition of maturation and survival of juvenile mice may lead to breeding season declines in abundance (Sadleir 1965; Healey 1967; Petticrew and Sadleir 1974; Fairbairn 1977; Galindo and Krebs 1987).

The southern red-backed vole (*Clethrionomys gapperi*) (see Kryštufek et al. 2020 for change in genus name) is a common microtine that coexists with *P. maniculatus* in temperate and boreal forests across North America and may be a potential competitor (Morris 1996). In terms of competition for space, several studies concluded that voles of the genus *Microtus* seem to exclude *P. maniculatus* from grassland habitats, at least in some situations (Redfield et al. 1977; Abramsky et al. 1979; Hallett et al. 1983). However, the northern red-backed vole (*C. rutilus*) and meadow vole (*Microtus pennsylvanicus*) seemed to have no effect on spatial distribution or abundance of deer mice in boreal white spruce forests of the Yukon (Gilbert and Krebs 1984; Galindo and Krebs 1985). Similarly, Wolff and Dueser (1986) concluded that *C. gapperi* and *Peromyscus* exhibited non-competitive coexistence in broadleaved forest in Virginia where the former species selected rocky outcrops as habitat and the latter selected forest. In terms of competition for food, both the deer mouse and the southern red-backed vole have very broad diets that overlap extensively (for deer mice, see Martell and Macauley 1981; for voles, see diet review in Boonstra and Krebs 2012), and thus, there is the potential for direct limitation of one species by the other. We ask here if long-term monitoring of population changes of these two species in undisturbed forest might indicate if deer mice decline in abundance when numbers of red-backed voles are substantially higher.

We report on a 26-year record (5–6 sampling periods each summer) of changes in abundance and demography of *P. maniculatus* in old-growth coniferous forest in southern BC from 1995 to 2020. Our objectives were (1) to provide a description of demographic changes; and (2) to evaluate three separate hypotheses (H) that may explain those changes during this 26-year period: (H_1) high food abundance–autumn cone crops of Douglas-fir and interior spruce (*Picea glauca* x *P. engelmannii*) will be followed by good

winter survival and peak abundance in the next summer and autumn; (H_2) spring reorganization will lead to breeding season declines in abundance; and (H_3) interspecific competition between deer mice and red-backed voles cause deer mice to be lower in density when voles are higher.

For the food hypothesis H_1, we predicted that increased food supply from fall masting of Douglas-fir and interior spruce would enhance overwinter survival of *P. maniculatus* and increase reproductive output in the following summer breeding period. Therefore, deer mouse densities should be higher in the summer and fall periods following conifer masting compared to years of low seed production. For the social interaction hypothesis H_2, we predicted that spring reorganization via density-dependent inhibition of maturation and survival of juvenile mice would lead to breeding season declines in abundance of *P. maniculatus*. For the competition hypothesis H_3, if there is some interference competition between deer mice and red-backed voles, we predict that fewer deer mice would occur on sites of relatively uniform and continuous forest habitat if red-backed voles are present in substantial numbers.

Materials and methods

Study area

The study was located in the Bald Range 25 km west of Summerland, BC (49^0 40′ N; 119^0 53′ W) in the upper interior Douglas-fir (IDF$_{dk}$ = dry precipitation regime, cool temperature regime) and montane spruce (MS$_{dm}$ = dry precipitation regime, mild temperature regime) biogeoclimatic zones (Meidinger and Pojar 1991). The area has sandy loam soils with gently rolling topography at 1450 to 1520 m elevation above sea level (a.s.l). The 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 (Meidinger and Pojar 1991). Snow cover is usually present from late October to early May. Open to closed canopy mature forests of Douglas-fir cover much of the IDF zone, with even-aged post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) stands at higher elevations. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which regenerated after wildfire 100–150 years ago. Hybrid interior spruce and subalpine fir (*Abies lasiocarpa*) 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).

The study was conducted in a commercial forest landscape covering 10,000 ha and was a mosaic patchwork of various post-harvest (4- to 42-year-old successional forests) and old-growth stands of 10 to 100 + ha composed of the four 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. Clearcut 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 mountain pine beetle (MPB) (*Dendroctonus ponderosae*) and continued to 1984 (Sullivan et al. 2010). Periodic 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 study area.

To sample *P. maniculatus* in relatively undisturbed old-growth forests, we installed one trapping grid in each of three stands that were separated by an average of 1.79 km (range 0.67–2.96 km) in May 1995. A measure of independence of these grids was that only 4 of 1295 (0.31%) individual deer mice moved among grids. All stands were composed of a mixture of Douglas-fir, lodgepole pine, interior spruce, and subalpine fir. The latter two species were particularly common in wetter sites. Grids in two 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 four conifer species. The mean (± SE) density of overstory (> 3 m height) conifers was 1402 ± 361 stems/ha and for all conifers was 2092 ± 498 stems/ha. Overstory density (conifers > 3 m in height) was maintained at a mean (± SE) of 1437 ± 386 stems/ha after moving the grids in 2010. Canopy closure ranged from 82 to 88% in these three forest stands, and hence, understory herb and shrub layers were relatively depauperate (Sullivan et al. 2017). Pinegrass (*Calamagrostis 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.

Trapping protocol

Deer mouse and southern red-backed vole populations were sampled 5–6 times per summer (at 4-week intervals) from May or June to October 1995 to 2020. One live-trapping

grid (1 ha) was in each stand. Each grid 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 and left in position until the next trapping period 4 weeks later. All mice captured were ear-tagged with serially numbered tags, breeding condition determined (males: scrotal or not; females: non-reproductive, pregnant, or lactating), weighed on Pesola spring balances, and point of capture recorded. Animals were released on the grids immediately after processing. The duration of the breeding season was determined if males were reproductive and females lactating (Krebs et al. 1969). A pregnancy was considered successful if a pregnant female captured in 1 month was recaptured lactating in the following month. Short-tailed (*Mustela erminea*) and long-tailed (*M. frenata*) weasels were occasionally captured in live-traps and provide an index of abundance and measure of potential predation on deer mice. 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.

Population data analyses

Abundance estimates were derived from the Jolly-Seber (J-S) stochastic model for open populations with small sample size corrections (Seber 1982; Krebs 1999). The number of individual mice captured was used as the population estimate for the first and last sampling weeks. We calculated the effective trapped area (ETA) for *P. maniculatus* on each grid based on mean maximum distance moved (MMDM) as a boundary strip method (Krebs et al. 2011). Estimates of population size were converted to a density estimate by dividing population estimates for each trapping period by the ETA. Mean ETAs were 1.56, 1.69, and 1.73 ha for the three grids. We consider each of these estimates to be a "density index" (Krebs et al. 2011). Jolly trappability was calculated according to Krebs and Boonstra (1984). We compared J-S and spatially explicit capture recapture (SECR) estimates for the first three years (1995 to 1997) and found close agreement: linear regression $R^2 = 0.67$, $n = 48$, $P < 0.001$. Figure in Supplementary data and materials.

P. maniculatus were classified as juveniles (≤ 20 g) and adult (≥ 21 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 productivity were derived from the sample of animals captured in each trapping session and then summed for each summer 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), calculated as number of male and female juvenile mice captured each summer divided by the number of lactating females caught in that summer. The proportion of young-of-the-year that was in breeding condition in the summer of their birth was calculated for both males and females. These mice 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 days) for summer (May to October) and winter (November to April) were estimated from the Jolly-Seber model and represent both mortality and emigration (chapter 2; Krebs 1999). Overwinter survival rates for 2009–2010 were not available for two grids that were moved to new forest stands in May 2010. For year t, summer population growth was the fall estimate (t)/spring estimate (t), and winter population change was the spring estimate ($t+1$)/fall estimate (t).

Coniferous cone crops

There were no reports of seed availability for the exact study area, but information was available from a wider geographic 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 1 "heavy" and 3 "moderate" cone crops in both Douglas-fir and spruce, in the Okanagan-Thompson area over the 26-year period of our study (A. Vyse, pers. obs.). Subalpine fir was a minor tree species in or near our study stands, and hence, we did not include cone crop data for that species.

The one "heavy" and three "moderate" cone crops of Douglas-fir and spruce over the 26-year period were collected at the Opax Mountain and Sicamous Creek silvicultural system sites, respectively. The Opax site was near Kamloops, BC (50° 48′ N, 120° 27′ W), and the Sicamous site was near Sicamous, BC (50° 50′ N, 119° 50′ W), 132 km and 146 km from our study area, respectively. The Opax forest is in the interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991) and is representative of the very dry hot and dry cool subzones (IDF_{xh} and IDF_{dk} respectively) described by Lloyd et al. (1990). The site elevation ranges from 900–1100 m a.s.l. (Mud Lake) and 1200–1300 m a.s.l. (Opax Mountain). The Sicamous 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 1530 to 1830 m a.s.l.

Ten seed traps (initially 0.64 m^2 and 0.25 m^2 after 10 years) were installed in each of three relatively undisturbed stands of old-growth Douglas-fir (Opax) and spruce subalpine fir (Sicamous) in the summer of 1995. Following collection of Douglas-fir and spruce 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).

We also investigated other general sources of cone crop data for Douglas-fir in the Okanagan-Thompson area (36,000 km^2). Cone collections of Douglas-fir occurred throughout the 26-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 have quantitative amounts of Douglas-fir seed per ha from Opax Mountain, as well as relative overall amounts from year to year across the region.

Within each of the genera, *Abies*, *Picea*, *Pinus*, and *Pseudotsuga* cone crops were synchronous across wide (e.g., up to 2500 km for *Pinus*) geographic regions of the Northern Hemisphere (Koenig and Knops 1998, 2005). The heavy crops of Douglas-fir and spruce during this 26-year period were widespread in southern BC based on the general cone surveys (A. Vyse, pers. obs.). Low and moderate size crops also followed this pattern. Douglas-fir seed falls in September–October and spruce seed-fall occurs over the winter.

Statistical analyses

Spectral analysis (NCSS 2021) was applied to the annual density estimates to test for cyclicity in the deer mouse abundance data. We explored the multiple regression relationships (NCSS 2021) between the 19 annual parameters available for our 25 study years, and we averaged our three study locations on the assumption that the same parameters affecting deer mice are regional in operation (Supplementary Materials). Monthly temperature and precipitation data are for Penticton, BC, Canada, from Environment Canada records. Our analysis was done in two stages. Using the "All Possible Regressions" module, we selected the regression parameters that minimized the RMSE (root mean square error). Typically, this module highlighted the three best parameters for a multiple regression to predict summer increases or winter declines of *P. maniculatus*. We then used the robust regression module in NCSS (2021) to predict the best statistical models for our data (detailed results in Supplementary Materials).

Specifically, we asked what variables could be used to predict the summer finite rate of increase and the winter finite rate of decline. As independent variables, we used the density of deer mice and red-backed voles, and only for deer mice: the summer survival rate, the winter survival rate, the proportion of females lactating in summer, the number of total new adults and juveniles recruited, an index of juvenile production, seed crops of Douglas-fir and white spruce, total seed crop for each year, and an index of weasel abundance for the year. For all regression graphs, the inner cloud is the 95% *confidence limits* for the estimated mean regression line, and the outer wider belt is the 95% *prediction limits* for any individual point of data you may add in the future. The prediction limits are always wider than the confidence limits for all regression lines. All limits are 95% (NCSS 2021). Mean values and 95% confidence intervals (IBM Corp. 2021) were calculated for all demographic parameters to compare high and low years for *P. maniculatus* populations. In all analyses, the level of significance was at $P = 0.05$ (Zar 1999).

## Results

Deer mouse populations

We conducted 145 trapping periods from June 1995 to September 2020 on the three grids. The total number of individual *P. maniculatus* captured was 1295. Other forest floor small mammal species included the southern red-backed vole and occasional captures of the northwestern chipmunk (*Neotamias amoenus*), montane shrew (*Sorex monticolus*), and masked shrew (*S. cinereus*). The overall mean ($\pm$ SE) trappability (likelihood of capture on any given trap-night) estimates of *P. maniculatus* were 79.5% $\pm$ 2.9, 78.7% $\pm$ 3.4, and 79.9% $\pm$ 3.8 for the three grids.

During spring, mean abundance was 2–3 mice per ha with numbers < 1 per ha in 1999, 2010, 2012 to 2015, and 2018 (Fig. 1). Mean densities increased 2.5 to 3.4 times from spring to fall. Based on mean annual peak numbers in autumn, there were five identifiable population peaks over the 26-year period with relatively high populations in 1996, 2001, 2005–2007, 2015–2016, and 2019 (Fig. 1). These peaks were separated by 5, 4, 8, and 3 years and reached estimated mean annual peak numbers of 10, 10, 11, 8, and 13 per ha, respectively. A spectral analysis indicated a 5-year cyclic fluctuation in mean annual abundance of deer mice (Fig. 2). The overall mean abundance and the mean annual peak abundance were both significantly higher (non-overlapping 95% CIs) (1.8 and 2.1 times, respectively) in high than low years (Table 1). Deer mouse mean numbers increased or remained similar from fall to the next spring in only 2 of 25 overwinter periods (1995–1996 and 2018–2019); otherwise,
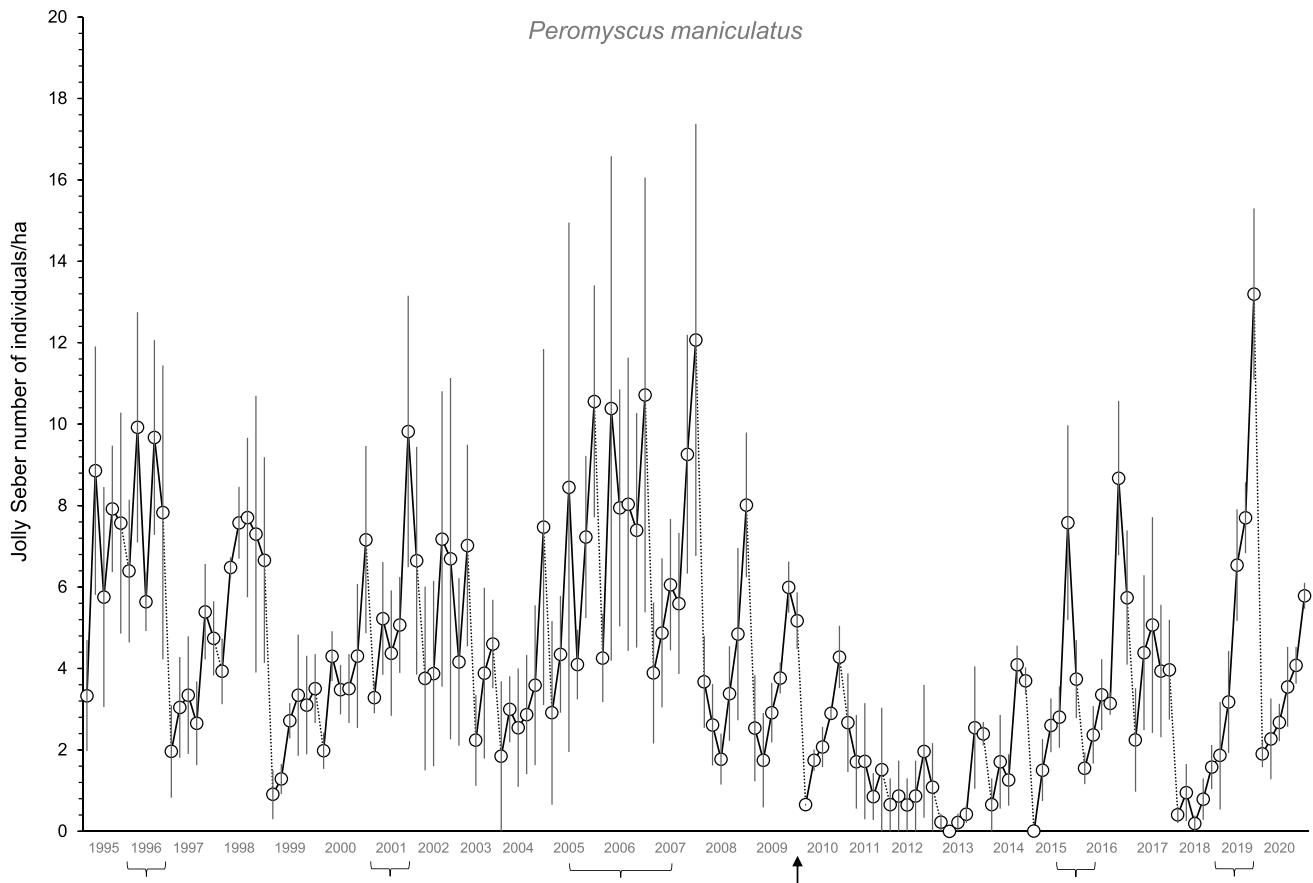
Fig. 1 Mean ($n = 3$ replicate sites $\pm$ SE) number of *P. maniculatus* per ha as an index based on Jolly-Seber population estimates and effective trapped area 1995 to 2020 in old-growth forest in southern British Columbia, Canada. Data points indicate individual trapping weeks each summer (May to 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
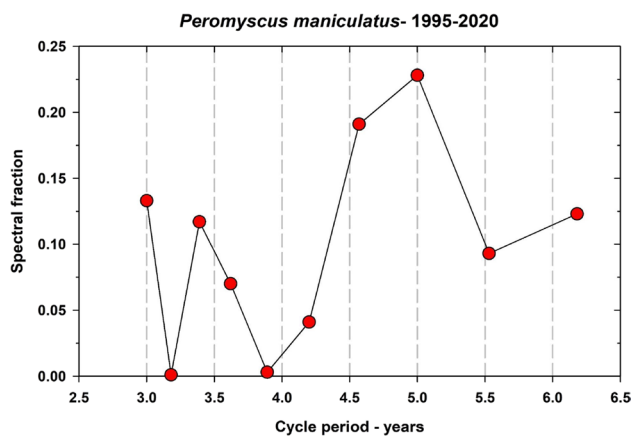
Fig. 2 Spectral analysis of mean annual abundance of *P. maniculatus* and cyclic periods over the 26-year period 1995 to 2020 depicting a 5-year cyclic population fluctuation in numbers

there were dramatic overwinter declines in all years (Fig. 1). The mean abundance declined during the breeding season in

16 of 26 years, but in 9 of these, it was a moderate decline, with substantial loss (mean of 50.8%) of mice in the other 7 seasons: 1995, 1996, 2005, 2006, 2013, 2017, and 2018 (Fig. 1).

Demographic responses

Mean number of lactating females (successful pregnancies) and mean number of recruits per year between periods of "high" and "low" numbers of mice provided a measure of reproductive performance (Table 1). Deer mice had significantly (non-overlapping 95% CIs) more juvenile recruits and total recruits in high than low population years (Table 1; Fig. 3). The mean number of successful pregnancies per year also followed this pattern. The overall mean ($\pm$ SE) percentage of adult females that were lactating was 69.4% $\pm$ 17.6. Of these reproductive females, 50.9% $\pm$ 10.2 (mean $\pm$ SE) had one litter only, 14.7% $\pm$ 0.4 had two litters, and the remainder (3.8%) 3 or 4 litters. The mean index of early juvenile productivity was 2.0 times higher in high (6.54 $\pm$ 1.46 surviving

Table 1 Mean ($n = 3$ replicate sites) $\pm$ SE estimates of demographic responses of *Peromyscus maniculatus* per year over 26 years in old-growth coniferous forest in British Columbia, Canada

Parameter	High years	Low years	Overall
Abundance/ha*	6.1 ± 0.6	3.3 ± 0.4	4.2 ± 0.4
Annual peak abundance/ha*	10.3 ± 0.6	5.0 ± 0.5	6.6 ± 0.6
Annual spring abundance/ha	3.0 ± 0.7	2.0 ± 0.3	2.3 ± 0.3
Population change in numbers			
Spring to Fall	3.23 ± 0.62	3.35 ± 0.57	3.31 ± 0.43
Fall to Spring	0.35 ± 0.04	0.43 ± 0.08	0.40 ± 0.05
Breeding season decline (%)	39.4 (3)	59.4 (4)	50.8 (7)
Number of lactating females	3.8 ± 0.4	2.2 ± 0.4	2.7 ± 0.3
Total recruits*	23.7 ± 1.7	13.4 ± 1.5	16.6 ± 1.5
Total juvenile recruits*	18.5 ± 1.5	10.0 ± 1.3	12.7 ± 1.2
Index of juvenile productivity	6.54 ± 1.46	3.33 ± 0.49	4.32 ± 0.62
Proportion of young-of-year breeding			
Males	0.05 ± 0.03	0.09 ± 0.02	0.07 ± 0.02
Females	0.12 ± 0.03	0.06 ± 0.03	0.08 ± 0.02
Summer J-S survival*	0.66 ± 0.02	0.67 ± 0.02	0.67 ± 0.02
(Rate per 28 days)			
Winter J-S survival*	0.78 ± 0.02	0.80 ± 0.01	0.79 ± 0.01
(Rate per 28 days)			
Number of years	$n = 8$	$n = 18$	$n = 26$

*Non-overlapping 95% CIs between high and low years

High years include 1996, 2001, 2005–2007, 2015–2016, and 2019; low years include 1995, 1997–2000, 2002–2004, 2008–2014, 2017–2018, and 2020. J-S, Jolly-Seber. Sample size in parentheses

young per female) than low (3.33 ± 0.49) years. There was no large difference in the proportion of young-of-the-year breeding in low versus high population years for either males or females (Table 1). Percentages of young deer mice remaining on the grids and breeding in their first summer of life were very low ranging from 5.0 to 12.0%.

Mean Jolly-Seber summer survival rates were similar when comparing these two periods of low and high abundance, as were winter survival rates between the two levels of abundance (Table 1). Mean monthly J-S summer survival was consistently lower (12%) than winter survival throughout the study with non-overlapping 95% CIs for all three comparisons (i.e., high, low, and overall populations) (Fig. 4; Table 1). Mean ($\pm$95% CI) overall survival rates were 0.67 (0.63–0.70) for summer ($n = 26$) and 0.79 (0.77–0.82) for winter ($n = 24$).

Coniferous cone crops

There were three relatively moderate to heavy crops of high-elevation spruce seed in 1997, 2003, and 2013, with a very heavy crop in 2018 (Fig. 5). Douglas-fir also had three moderate to heavy crops in 1995, 1999, and 2002, with a very heavy crop in 2018 (Fig. 5). Mean annual peak abundance of

P. maniculatus increased during summer-fall in the year after the first four substantial seedfall events in 1995, 1997, 1999, and 2002–2003 (Fig. 5). Deer mouse annual peak numbers declined in the following year in the first three cases. However, after the combined seedfall in 2002–2003, the mean annual peak abundance appeared delayed a year and then remained high (10–12/ha) for 3 years (2005 to 2007) before declining to a lengthy period of low numbers (2–6/ha). The gap in Douglas-fir seed production at Opax was the result of western spruce budworm (*Choristoneura occidentalis*) defoliation, but this insect was not present in our stands. The spruce seed crop in the fall of 2013 occurred when the mean abundance of *P. maniculatus* was already increasing during 2012 and 2013 before reaching relatively high mean annual peak numbers in 2015–2016 (Fig. 5). The combined heavy cone crops of both coniferous species in 2018 caused a dramatic increase in deer mice (13/ha in 2019) before numbers declined again in 2020. The major breeding season declines in 1995–1996 and 2005–2006 corresponded with the higher numbers of deer mice that had likely responded to coniferous seedfall (Figs. 1 and 5). Subsequent declines during reproductive periods were at substantially lower densities of mice.

Competition with red-backed voles

In terms of potential interference competition, there were four periods when peak populations of *C. gapperi* occurred on these forest grids: (1) 1997–1998, (2) 2004–2005, (3) 2011–2012, and (4) 2017–2018 (Fig. 6). Mean annual peak numbers of *C. gapperi* during these four periods were 2.6–4.7, 1.5–2.2, 13.7–16.9, and 4.9–8.2 times higher, respectively, than comparable measurements of density in *P. maniculatus* (Fig. 6).

Determinants of deer mouse population change

This analysis used multiple regression and found two significant relationships for population changes of deer mice during summer and winter periods. However, we could not predict average summer survival rates or average winter survival rates from any variables. The rate of summer increase was associated positively with mean summer temperature and the average density of red-backed voles in the same summer, and negatively with the proportion of females lactating over summer. Neither weasel abundance nor deer mouse population density were significant predictors of the summer rate of population growth of deer mice. Fig. 7 shows the observed and predictions for the summer increase. The standardized regression coefficients for the three predictor variables were nearly equal for this regression.

The rate of winter decline from autumn of year t to spring of year $t + 1$ could be predicted by three variables: positive association with summer rainfall of year t and total seed
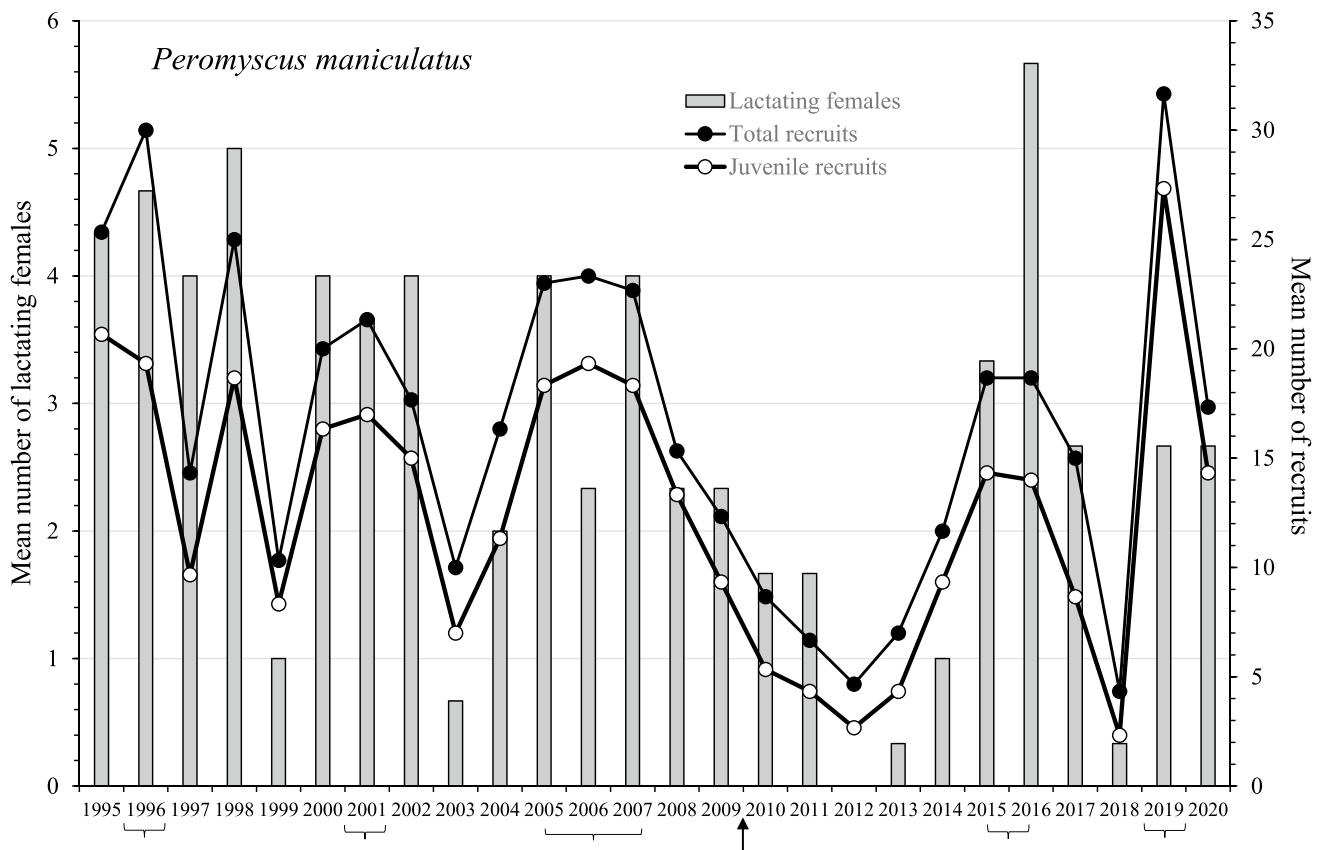
Fig. 3 Mean (*n*=3 replicate sites) number of juvenile and total recruits and number of lactating females (successful pregnancies) of *P. maniculatus* 1995 to 2020 in old-growth forest in southern Brit- ish Columbia, Canada. Years of "high" abundance are indicated along *x*-axis. Arrow indicates year of grid replacement

production in autumn of year *t*, and a negative association with the rate of summer increase in year *t*. Neither weasel captures nor deer mouse density in winter were significant predictors. Fig. 8 shows the observed and predictions for the winter declines. The standardized regression coefficient for seed production was twice as large as that for summer increase and summer rainfall of year (*t*) in this regression. Details are given in the Supplementary Materials.

Discussion

We report an intensive, long-term trapping program of *P. maniculatus* in old-growth coniferous forest in southern British Columbia. Based on mean annual peak density in autumn, populations of deer mice showed five periods of high numbers with intervals of 3 to 8 years between fluctuations over a 26-year period in old-growth coniferous forest. Mean density ranges of mice per ha reached maximums of 8 to 13 in autumn and minimums of 2 to 3 the following spring, thereby indicating the dramatic declines in numbers overwinter. This pattern of low annual variation in population density was like those of long-term (17 years) studies

in the Yukon (Gilbert and Krebs 1991) and southern Alberta (Millar and McAdam 2001). Similarly, most other studies of changes in abundance of *Peromyscus* across North America have reported a similar pattern of density from year to year with only very occasional irruptions (Terman 1968; Grant 1976; Fryxell et al. 1998; Lewellyn and Vessey 1998; Merritt et al. 2001).

The greater numbers of *P. maniculatus* in high than low years was directly related to number of successful pregnancies, total number of juvenile recruits, and a mean index of early juvenile productivity that was 37% higher. Temporary breeding season declines in abundance were common with up to 51% of mice lost in 7 of 26 summer seasons, and this likely contributed to the overall total summer survival of mice being consistently poorer (12%) than winter survival. Combined with very low proportions (5 to 12%) of young-of-the-year breeding and a relatively high proportion (51%) of adult females having just one litter, it may not be surprising that overall numbers of deer mice were generally low in this study. This pattern of second-year maturation of young deer mice was similar to reports from other northern and alpine environments where young mice never breed in their first

Seasonal survival of *Peromyscus maniculatus*
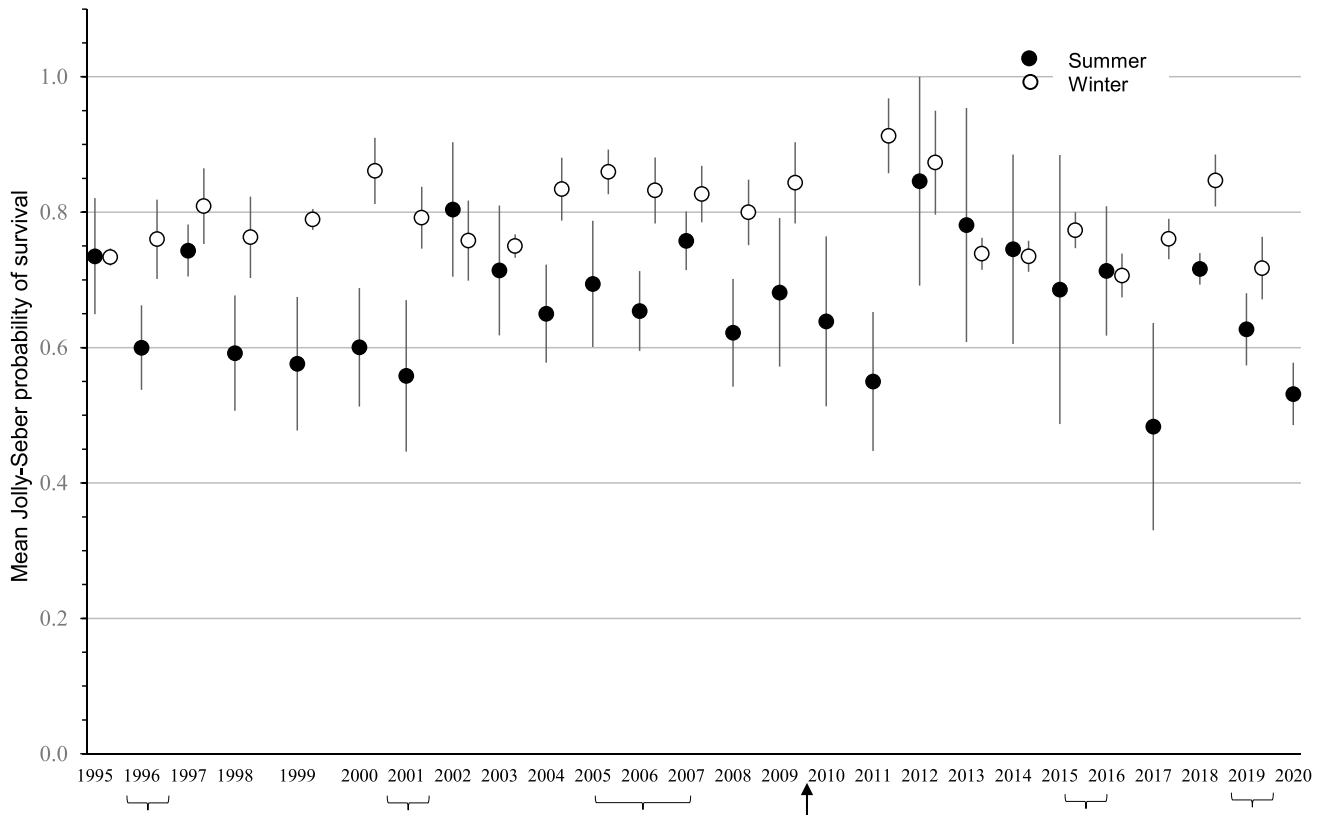
Fig. 4 Mean ($n = 3$ replicate sites $\pm$ SE) Jolly-Seber survival per 28 days of *P. maniculatus* as seasonal summer and winter periods each year 1995 to 2020 in old-growth forest in southern British Columbia, Canada. Years of "high" abundance are indicated along *x*-axis. Arrow indicates year of grid replacement

year (Van Horne 1982; Gilbert and Krebs 1991; Miller and McAdam 2001). Although our study grids were not considered as alpine or northern sites, they were at 1500 m a.s.l. elevation with a long winter of deep snow cover (up to 1 m or more) lasting from late October to early May. Thus, our relatively low densities and occasional short-term extirpations were perhaps not surprising based on a similar long-term record of *P. maniculatus* population changes in the Yukon. There deer mice fell to very low numbers for 6 years and declined to < 5 mice/ha over the subsequent 20 years (Krebs et al. 2018, 2019). Thus, our evidence argues that these forests are marginal most of the time for deer mice, and hence, this habitat constrains their life history. They breed once per summer or maximally twice, and if anything (e.g., low food, high conspecific density, high interspecific competition, or adverse weather) causes poor summer survival of young-of-the-year and of adults, then the population fails to increase.

Evaluation of the food supply hypothesis

We hypothesized (H_1) that increased food supply from fall cone crops of Douglas-fir and spruce would enhance overwinter survival, as well as enhance reproductive output in the next summer. It was partially supported for 5 of 6 seedfall events. The periods of high numbers in the next year ($t + 1$) generally followed a seed crop year t. Reproductive output was increased as measured by number of successful pregnancies, numbers of recruits, and index of juvenile productivity. However, in year $t + 1$, neither the proportion of young-of-the-year breeding nor summer population growth was affected by cone crops in autumn of year t. Winter population change of *P. maniculatus* in year t to $t + 1$ was significantly related to total coniferous seed crop of year t with a high ratio of spring to previous fall estimates of abundance suggesting a lower loss of mice in the winter after a cone crop.

In other studies, *P. maniculatus* responded positively to Douglas-fir seed in Oregon with respect to enhanced reproduction and abundance in summer-fall in the year after a seed crop (Gashwiler 1965, 1979). In several short-term summer seeding experiments with Douglas-fir seed, Sullivan (1979) reported that *P. maniculatus* increased in density up to 36 mice/ha with essentially unlimited amounts of seed. Similarly, an excess of white spruce seed in fall of year t
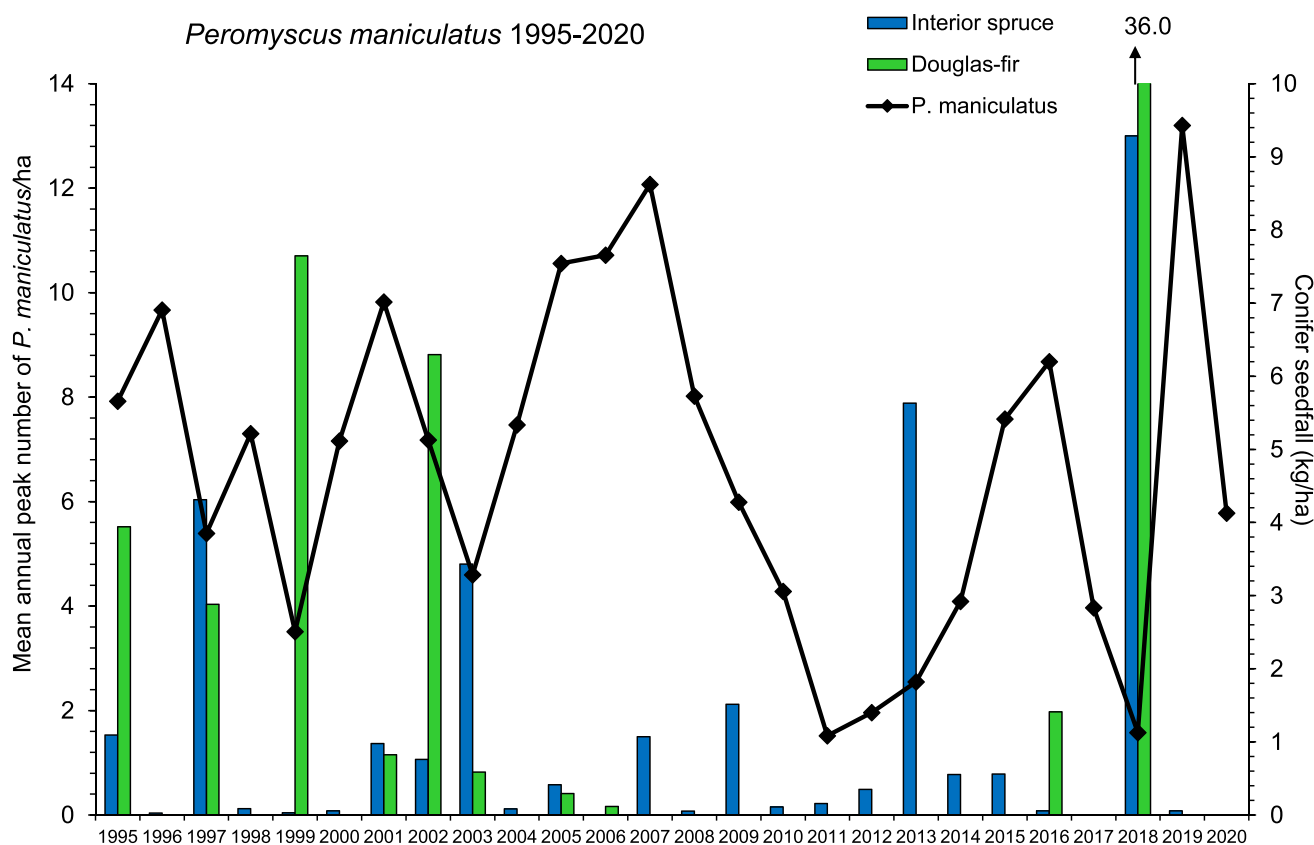
Fig. 5 Mean annual peak number of *P. maniculatus* per ha as an index during summer periods each year and seedfall (kg/ha) of Douglas-fir and spruce during 1995 to 2020 in old-growth forest in southern British Columbia, Canada. Seedfall mass for a given year was for the seedfall event in that year

increased the population of deer mice in year $t+1$ for one breeding season in the southern Alberta foothills (Lobo and Millar 2013). Both Douglas-fir and white spruce seeds provide high-quality food for deer mice based on caloric content and laboratory feeding trials (Smith 1967; Lobo and Millar 2011). However, Krebs et al. (2018) found no correlation between white spruce seed crops of year t and population changes in *P. maniculatus* in the Yukon overwinter of t to $t+1$ or in summer of year $t+1$.

Overall mean abundances of deer mice were 1.4 to 3.6 times higher in several clearcut sites (up to 4 to 6 years postharvest) than in uncut forest in a nearby study area (Sullivan and Sullivan 2022). In those clearcut sites with an abundance of lodgepole pine cones in logging slash, availability of pine seed created irruptions in deer mouse density in years immediately after harvest (Sullivan and Sullivan 2022), similar to what is seen in our area after a good natural cone crop. Other mast crops that increase *Peromyscus* abundance include sugar maple (*Acer saccharum*) in Ontario (Falls et al. 2007); acorn (*Quercus*) crops in Virginia (Wolff 1996); and acorn and red maple (*A. rubrum*) crops in Maine (McCracken et al. 1999; Elias et al. 2004). However, in all these studies, there were seasons or years when *Peromyscus*

populations either did not increase or declined in spite of substantial seed or mast crops (McShea 2000; Elias et al. 2004). Thus, heavy seedfall in year t does not always lead to population increases in year $t+1$ for *P. maniculatus*.

There are four important caveats to consider for our food supply hypothesis. First, the Douglas-fir and spruce seedfall data were collected from several locations in similar forest types as those in our study area, but some distance away. We have inferred that these same moderate and heavy seedfall events also occurred, at least to some degree, 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 observations of synchrony in cone crop survey data in southern BC.

Second, the effects of a substantial seed supply seemed to enhance survival in winter after the seedfall and also reproduction in the summer and fall of the next year leading to a high abundance year. There also could be a carry-over effect into a second year after the actual seedfall event, as indicated in 2000–2001 and 2004–2005 (Fig. 5). If seed supplies on the forest floor were exhausted in the winter and spring–summer immediately after the seedfall event, then
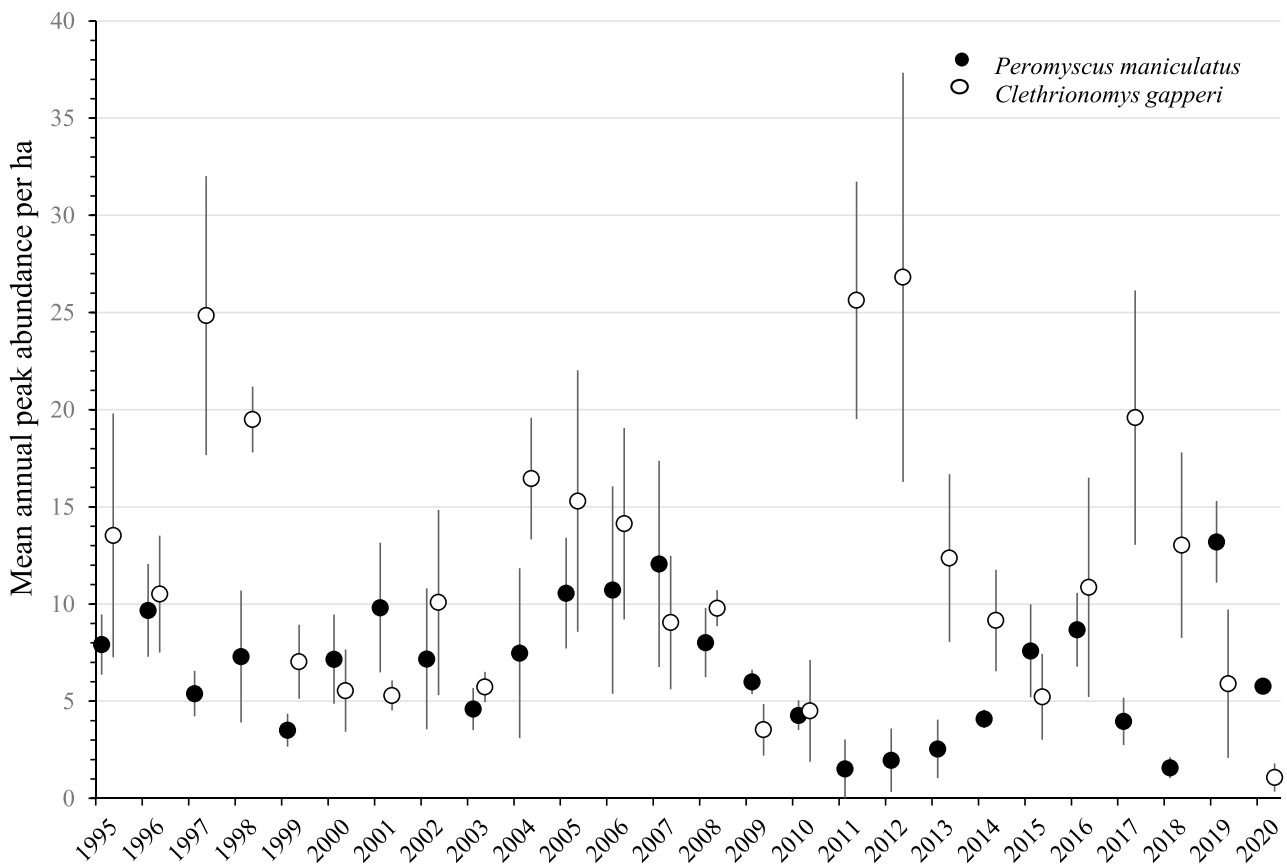
Fig. 6 Mean ($n = 3$ replicate sites $\pm$ SE) annual numbers of *P. maniculatus* and *M. gapperi* per ha as an index during summer periods each year during 1995 to 2020 in old-growth forest in southern British Columbia, Canada
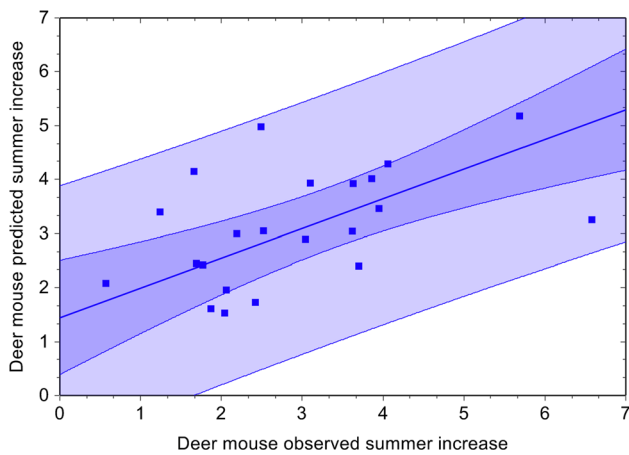
Fig. 7 Observed rate of summer population growth (fall density divided by spring density) in relation to that predicted by a three variable model including summer temperature, the proportion of females lactating and the abundance of red-backed voles. $R^2 = 0.59$, $n = 25$ years, $P \leq 0.02$. The shaded areas delimit 95% confidence limits and prediction limits. Details of the multiple regression are given in the Supplementary Materials
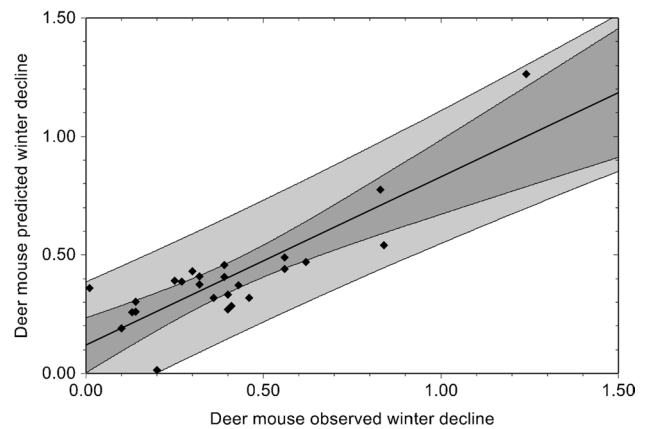
Fig. 8 Observed winter rate of population decline (spring density of $t+1$ divided by fall density of t) in relation to the predicted values from a three variable model including summer rainfall, total conifer seed production, and the rate of increase in the previous summer. $R^2 = 0.75$, $n = 25$ years, $P \leq 0.03$. The shaded areas delimit 95% confidence limits and prediction limits. Details of the multiple regression are given in the Supplementary Materials

some other factor such as an alternative food supply was responsible for the continued increase in mouse populations.

Third, red squirrels (*Tamiasciurus hudsonicus*) are a major seed predator of conifer seeds (Steele 1998) and likely competed with deer mice. The 2004–2011 period had minimal seedfall of Douglas-fir and spruce with mean numbers of squirrels ranging between 1 and 2/ha in the years 2006–2008 (Sullivan et al. 2010, based on 3 trapping grids). Similarly, mean numbers of red squirrels in 2014–2015 after a substantial seedfall of spruce in 2013 were at this same level of 1–2/ha (Sullivan et al. 2021). Thus, red squirrel abundance was relatively low, and it was unlikely that they were a major seed predator competing with deer mice in this ecosystem (but see Lobo and Millar 2013).

Fourthly, lodgepole pine is another coniferous species that may have contributed seed supplies to generate changes in deer mouse populations. The interior province-wide mountain pine beetle epidemic passed through our study area in 2008 resulting in tree mortality ranging from 19 to 40% in lodgepole pine stands. A "seed rain" in MPB-killed lodgepole pine stands occurs over 9 years or more after a MPB outbreak (Teste et al. 2011). The process of serotiny 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 (Teste et al. 2011). This potentially sustained "pine seed rain" may have enhanced populations of ground-foraging vertebrates such as *P. maniculatus* and other seed-eating species. However, we saw no evidence of a population response during the 5 years after 2008 when mouse numbers reached their lowest level. Another aspect of beetle-killed trees in lodgepole pine stands is an accumulation of fallen woody debris (branches and stems) on the forest floor that may generate positive responses for some forest floor small mammals with respect to food and cover. However, deer mice do not seem to respond positively to woody debris piles within standing forest or in clearcuts (Craig et al. 2006; Sullivan et al. 2012).

Evaluation of the social interaction hypothesis

We hypothesized (H_2) that spring reorganization resulted in poor survival of juvenile mice leading to breeding season declines in abundance. Deer mouse numbers declined in 16 of 26 summer breeding seasons and reflected the generally poor overall summer survival. In addition, there was a relatively modest mean proportion (69%) of adult females lactating (they may have bred, but lost their litter either in utero or while lactating), a high mean proportion (51%) of reproductive females with one litter only, and the almost complete lack of breeding by young-of-the-year. In terms of juvenile productivity, the overall mean of 4.32 juvenile mice per lactating female was slightly higher than expected based on a mean litter size in BC of 4.04 (range 1–9) (Banfield 1974). In the high population years, the higher index

(2.0 times) of juvenile productivity suggested that either litter sizes were increased, survival of young during lactation was higher, there were additional second and third litters, or immigration of juvenile mice into the grids was occurring, possibly in response to augmented food supply from cone crops in the previous years. Thus, this hypothesis was partly supported for a reorganization event that led to breeding season declines, and the cause may have been very poor survival of juvenile mice. The breeding season declines may arise from social strife among adult and juvenile mice that could lead to physiological changes that affect reproduction and survival of juveniles in year $t+1$ (Boonstra 1978, 1985; Galindo and Krebs 1987). Delayed maturation of juvenile mice was clearly in force in our populations, but the mechanism may be spacing behavior (e.g., spring reorganization) or, alternatively, lack of time to enter breeding status in the relatively short time period available for reproduction in high-elevation sites (Millar and McAdam 2001). A spring reorganization event may also result in dispersal of juvenile mice into suboptimal habitat in their first year of life, owing to negative social interactions with adult mice (Sadleir 1965; Healey 1967; Fairbairn 1977; Krebs and Boonstra 1978; Galindo and Krebs 1987).

Competition with red-backed voles

We hypothesized (H_3) that *P. maniculatus* will be at lower abundance when the red-backed vole is present at equal or higher numbers. Peak populations of *C. gapperi* (Sullivan et al. 2017) ranged from 1.5 to 16.9 times higher than concurrent measurements for *P. maniculatus* and hence tended to support H_3. However, the relationship between *C. gapperi* density was positive but weak for summer rates of change in *Peromyscus*, and there was no significant effect of *C. gapperi* density on winter declines of deer mice, thus calling into question how strong the interaction is between these two species in our study area. Our sampling grids were in relatively uniform and continuous coniferous forest without apparent macrohabitat diversity. Thus, habitat selection may not have been an important factor for these two species which have in general similar diets in coniferous forests: fungi during summer and fall, conifer seeds and berries during fall and winter months, and miscellaneous plant parts, lichens, and arthropods year-round (Merritt 1981; Gunther et al. 1983; Ovaska and Herman 1986; Lobo et al. 2009; Boonstra and Krebs 2012). In experimental studies, *C. rutilus* and meadow voles had no effect on the spatial distribution or abundance of deer mice in white spruce forest in the Yukon (Gilbert and Krebs 1984; Galindo and Krebs 1985) or for *C. gapperi* and deer mice in broadleaved forest in Virginia (Wolff and Dueser 1986). However, Merritt et al. (2001) concluded from a 20-year study in the eastern deciduous forests of North America that intra- and inter-specific

competitive interactions between deer mice and voles were the basis of their population dynamics. Lemaitre et al. (2010) concluded that deer mice may exclude *C. gapperi* in recently harvested forests (e.g., clearcuts), but this result may have little bearing on actual competition between these two rodent species in undisturbed forest.

Conclusions and future research

Tentative conclusions, based on our long-term observational results, about changes in our deer mouse populations were that they had (1) relatively low densities per ha ranging from 8 to 13 for mean annual peak numbers in fall and dropping to 2 to 3 by the following spring; (2) a 5-year cyclic fluctuation in abundance that may be related to pulsed food supplies in the form of coniferous seeds; (3) clear and consistent breeding season declines that presumably result from density-related social inhibition; (4) very poor survival of both sexes; (5) an almost complete lack of breeding by young of the year; and (6) possibly weak interference competition with *C. gapperi* resulting in slightly reduced *Peromyscus* densities during *C. gapperi* peaks.

Future research in these old-growth forests should have two approaches. First, basic natural history is related to diet and to spatial organization. The deer mouse is an ideal species since it has breeding season declines and is a major predator of conifer seeds. The seasonality and relationship to weather of other foods such as berries, related plant products, invertebrates, and fungi in driving population dynamics should also be investigated. We suggest that intensive radiotelemetry of both species (males and females) would give insight into spatial overlap within and between species as a function of variation in breeding condition and food abundance. Second, large-scale year-round field experiments should test the overwinter food, spring reorganization, and competition hypotheses. In particular, food supplementation experiments are needed to investigate both "pulsed" and "continuous" feeding regimes for 5 to 10 years to determine the carry-over effect of food supplies (e.g., conifer seeds) as suspected in this study.

Declarations

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