

ORIGINAL ARTICLE



Long-term monitoring of cycles in *Clethrionomys rutilus* in the Yukon boreal forest

Charles J. KREBS,¹ Alice J. KENNEY,¹ B. Scott GILBERT² and Rudy BOONSTRA³

¹Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada, ²Renewable Resources Management Program, Yukon University, Whitehorse, Yukon, Canada and ³Department of Biological Sciences, University of Toronto Scarborough, Toronto, Ontario, Canada

Abstract

Baseline studies of small rodent populations in undisturbed ecosystems are rare. We report here 50 years of monitoring and experimentation in Yukon of a dominant rodent species in the North American boreal forest, the red-backed vole *Clethrionomys rutilus*. These voles breed in summer, weigh 20–25 g, and reach a maximum density of 20 to 25 per ha. Their populations have shown consistent 3–4-year cycles for the last 50 years with the only change being that peak densities averaged 8/ha until 2000 and 18/ha since that year. During the last 25 years, we have measured food resources, predator numbers, and winter weather, and for 1-year social interactions, to estimate their contribution to changes in the rate of summer increase and the rate of overwinter decline. All these potential limiting factors could contribute to changes in density, and we measured their relative contributions statistically with multiple regressions. The rate of winter decline in density was related to both food supply and winter severity. The rate of summer increase was related to summer berry crops and white spruce cone production. No measure of predator numbers was related to winter or summer changes in vole abundance. There was a large signal of climate change effects in these populations. There is no density dependence in summer population growth and only a weak one in winter population declines. None of our results provide a clear understanding of what generates 3–4-year cycles in these voles, and the major missing piece may be an understanding of social interactions at high density.

Key words: boreal forest, climate change, density dependence, population cycles, predation, winter severity

INTRODUCTION

As climate changes and humans cause habitat disturbances around the globe, a plea has gone out for long-term monitoring of populations and ecosystems (Lindenmayer & Likens 2009; Lindenmayer *et al.* 2012; Hughes

et al. 2017). To achieve this, goal two major obstacles must be overcome. First, one needs a relatively undisturbed ecosystem of sufficient area to contain the species interactions that occur there (Sinclair 1998). Second, secure research funding is required for a long time. Since much science funding flows for only 3–5 years, there is a disincentive to researchers to initiate long-term monitoring studies. We have been fortunate in this case to have been invited to the Kluane region of the southwestern Yukon in 1973 to carry out a species inventory of small rodents (Krebs & Wingate 1976). Once there, we

Correspondence: Charles J. Krebs, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada. Email: krebs@zoology.ubc.ca

found an undisturbed ecosystem with many small rodent species and a dominant herbivore in the snowshoe hare (*Lepus americanus*). Since 1976, we have studied both the rodents and the snowshoe hare to gain an understanding of the vertebrate food web in this part of the boreal forest (Boutin *et al.* 1995; Krebs *et al.* 2001; Boonstra *et al.* 2018). We report here one part of these Yukon studies, an attempt to understand the population dynamics of the most common small rodent in this part of the boreal forest, the northern red-backed vole, *Clethrionomys rutilus* (Boonstra & Krebs 2006, 2012; Boonstra *et al.* 2016; Boonstra *et al.* 2018), a 25-g rodent that breeds only in summer and rarely lives longer than 1 year. There has been much controversy over the mechanisms driving population changes in small rodents (Andreassen *et al.* 2021), and we take here a more comprehensive approach of attempting to measure the major components of controversy, food supply, predation, weather, and inferred social dynamics as elements in population changes of the red-backed vole in the southern Yukon of Canada. We treat this analysis as an exploratory data analysis since we have not been able to manipulate over 25 years' food supplies, predator numbers, or weather, and have been able only in a few cases to do short-term food and social interaction experiments. The expectations in the small rodent literature are that food supplies and predation should be strong determinants of population changes and that severe winter weather should reduce populations, so that climatic warming should be visible in overwinter losses. There is much speculation about social effects on rodent population changes but few experiments to shed light on this factor except in laboratory experiments (Andreassen *et al.* 2021).

MATERIALS AND METHODS

Red-backed voles were live-trapped in the Yukon Klunane boreal forest over 2 days with Longworth live-traps, marked, and released on two to four long-term control grids that were each laid out on a 10×10 array with 15-m spacing, as described in Gilbert and Krebs (1981) and Boonstra *et al.* (2001). Three checks over 2 days (morning, evening, morning) were made to calculate the density with the ML estimator in Murray Efford's *Density 5* program (www.otago.ac.nz/density/). During phases of low density when only one to three individuals were captured on a grid, we used minimum-number-alive to estimate density. Minimum trappability (Krebs & Boonstra 1984) averaged 85% over all years, but very young juveniles could not be live-trapped before 4 weeks of age. Some trapping grids were moved short distances (<20 km) over

the years, but one control (Grid J) was set out in 1979 and trapped ever since (Gilbert & Krebs 1981, 1991). Local grid populations always fluctuated closely in phase ($r = 0.89$, $n = 94$). Here, we will analyze only the spring and fall estimates of density and define *summer population change* as fall density/spring density, and conversely *winter population change* as spring density (t)/autumn density ($t-1$). Instantaneous rates of change were calculated as \log_e of these finite rates.

Measurements of food supplies began in 1986 for white spruce (*Picea glauca*) cones following the protocol of LaMontagne *et al.* (2005) with an average sample of 700 trees per year. Ground berries, mushrooms, and soapberries were sampled from 1997 onward. Ground berries consisted of five major species: bearberry (*Arctostaphylos uva-ursi*), red bearberry (*A. rubra*), crowberry (*Empetrum nigrum*), cranberry (*Vaccinium vitis-idaea*), and toadflax (*Geocaulon lividum*) (Boonstra *et al.* 2017). All were counted in 40 × 40 cm fixed quadrats in late July and early August beginning in 1997 with an average sample size of 700 per year (Krebs *et al.* 2009). Aboveground mushroom biomass was estimated each year in 600 plots of 28 m² (Krebs *et al.* 2008). Soapberries (*Shepherdia canadensis*) were counted and weighed each summer on 217 single stems averaging 10 mm in diameter.

Predator numbers were indexed by winter snow tracking over the same 24-km trail each winter since 1987 after new snowfalls (O'Donoghue *et al.* 2022). The major mammal predators on small mammals are coyotes (*Canis latrans*), ermine (= weasel, *Mustela erminea*), and marten (*Martes americana*). The latter were common only after 2000. Least weasels (*Mustela nivalis*) were very rare. Voles are also taken by birds of prey, but we do not have a good long-term index of their diets or numbers (but see Doyle & Smith 2001; Rohner *et al.* 2001).

Weather records of monthly temperatures and precipitation were obtained from the Haines Junction Weather Station of Environment Canada since 1973. In 2005, we began to measure temperatures directly on our study area with Thermocron buttons every 4 h from ground level to 80 cm to measure winter severity and its possible effects on voles and mice. We designed a measure of *winter severity* by measuring the number of degree-days below -10°C at ground level from November to March by use of temperature data collected at six sites on three control live-trapping grids.

We explore here four potential limiting factors for red-backed vole density changes: winter weather, food supplies, predator numbers, and density-dependence. The resulting data sets include red-backed vole rates of density change over winter and summer, weather records, indices

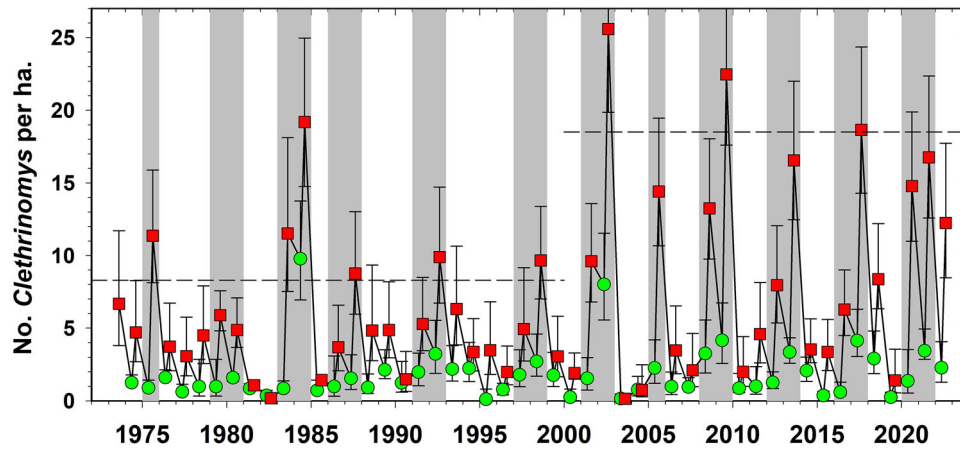


Figure 1 Changes in red-backed density on control grids at Kluane Lake, Yukon from 1973 to 2022. Green circles, spring density; red squares, autumn density. Average 95% confidence limits plotted. Shaded areas are cyclic peaks. Dashed horizontal line shows the average peak density for all years before (8.3/ha) and after 2000 (18.4/ha).

of major potential food items, and predator indices for the two main mammal predators. Given these data were collected over a variable number of years ranging from 25 to 50, we applied robust multiple regression in NCSS 2022 (www.ncss.com) after screening all possible explanatory variables in the All Possible Regressions routine. The number of variables (p) used in the selected regression was restricted to those with Mallows' $C_p < p + 1$ with a minimum value of square root mean square error. These choices typically maximize R^2 values for the multiple regression. While evaluating these statistical models based on observational data, we must recognize that predictive statistical models are not causal inference (Arif & MacNeil 2022).

RESULTS AND DISCUSSION

Fig. 1 shows the changes in spring and autumn red-back vole density on control sites over 50 years from 1973 to 2022. The 3–4-year cycle continues, possibly with an increase in peak density since the year 2000. Peak densities from 1973 to 2000 averaged 8.3 per ha with a range of 3.5 to 19.7. From 2000 to 2022, peaks averaged 18.5 voles per ha with a range of 14.4 to 25.6, more than double the earlier period. We subdivide the data shown in Fig. 1 into periods of summer population growth and periods of winter population decline and analyze how each of these two rates is related to our environmental measurements.

1. Winter population change in density

Winter population changes were measured from the change in density from late September to early October (year $t-1$) to May (year t) on two to three control grids.

Instantaneous rates of winter population declines averaged -1.33 (range -5.11 to $+1.11$) over the 48 years of complete data from 1974 to 2022. Winter population density increased in 5 of the 48 years sampled because of late summer juvenile recruitment occurring after the fall trapping in late September. However, the broad pattern is that winter rates translate into finite rates of decline from autumn to the next spring averaging 76% ($n = 48$).

We estimated the best combination of variables that could predict winter population changes. Ten variables were available: food item production from the previous summer, including aboveground mushroom biomass; berry counts from bearberry, red bearberry, crowberry, cranberry, and toadflax; soapberry production; white spruce cone counts; weasel and marten abundance in the current winter; and winter severity in the current winter. Winter severity was estimated from the number of degree-days less than -10°C at ground level from November to March and ranged from 28 in 2004–2005 to 462 in 2012–2013. Fig. 2 shows the resulting observed and predicted points for each year utilizing three variables: aboveground mushroom biomass and bearberry counts from the previous summer and winter severity from the current winter. The best predictive equation ($R^2 = 0.59$) was:

$$\begin{aligned} \text{Instantaneous overwinter change in density} = & -3.4805 + \\ & (0.004263 \times \text{winterseverity}) \\ & + (0.01678 \times \text{Mushrooms}_{\text{lag}1}) + (0.052126 \times \text{Bearberry}_{\text{lag}1}) \end{aligned}$$

where lag1 indicates the data from the previous summer growing season.

The general conclusion is that winter declines are a function of winter food supplies and winter weather, but

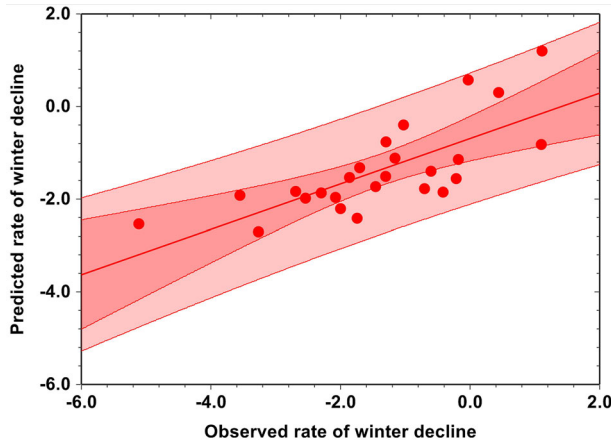


Figure 2 Observed and predicted winter instantaneous rate of population decline over 7 months from October to May from 1997 to 2022. The three best predictive variables are food supplies from the previous summer (aboveground mushroom biomass and bearberry counts) and winter severity, $R^2 = 0.59$, $n = 25$ years. An instantaneous rate of 2 is equivalent to about a sevenfold increase in density, while a rate of -6 is more than a 99% decline overwinter.

the winter severity result violates the common belief that northern rodent populations are strongly affected by more severe winter weather. Weasel and marten abundance in winter showed no significant relationship with the intensity of winter declines in red-backed voles. The complete multiple regression analysis is given in the Supporting Information.

One surprising result from our studies is that predation seems to play only a minor part in explaining population changes in our red-backed voles. There is much discussion in the small mammal literature about the role of predation in causing population changes (Korpimäki *et al.* 2005; Fauteux *et al.* 2016). One possible explanation is that when small mammals are at low density in our study area, there is insufficient food to support many small mammal predators, which effectively go locally extinct.

Since we do not know the diet of red-backed voles in winter (except that it does not seem to be spruce seeds, see Boonstra & Krebs 2006), we assume that the two vegetation variables are indicators of good and bad years for winter food supplies. Bearberry, a key contributor to the predictions and a very common ground berry, does not occur everywhere in the Kluane boreal forest and probably serves as a general indicator of the preferred berry productivity in this forest. Red-backed voles are known to eat mushrooms when they are available in summer,

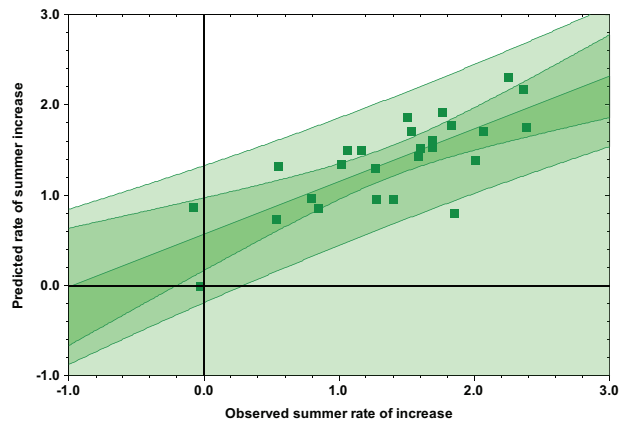


Figure 3 Observed and predicted summer instantaneous rate of population increase from May to October from 1997 to 2022. The four best predictive variables are food supplies from the berry crops of cranberry, toadflax, total berry counts, and the white spruce cone crop of the current year, $R^2 = 0.69$, $n = 25$ years.

so the association with overwinter survival could reflect plant productivity associated with soil moisture. Krebs *et al.* (2008) found that epigeous mushroom productivity in this area is correlated with rainfall early in the growing season.

1. Summer population change in density

Red-back voles increase in density from spring to fall from breeding. Overwintering adults can have two to four litters over the summer, and in some years, juveniles from the first litter can also breed once. Typically, however, young-of-the-year do not breed until the summer following their birth. We measured summer increases from May to September each year on two to three control grids. We estimated the best combination of variables that could predict summer rates of population growth with the 10 variables listed above. Fig. 3 shows the observed and predicted rates of summer increase from four variables: berry crops of cranberry, toadflax, total berry counts of all groundberries, and the white spruce cone crop of the current year. The best predictive equation was:

$$\begin{aligned} \text{Instantaneous summer increase in density} = & 2.6095 + \\ & (0.03619 \times \text{Cranberries}) - (0.02291 \times \text{Toadflax}) - \\ & (0.01468 \times \text{Allberries}) - (0.07217 \times \log_e(\text{spruceconecount})) \end{aligned}$$

where all variables were measured in the current year.

The conclusion is that summer rates of population growth of red-backed voles are largely determined by food supplies in each summer. Since spruce seeds are unlikely to be a critical element in the diet (Boonstra & Krebs 2006), we assume it enters this predictive equation

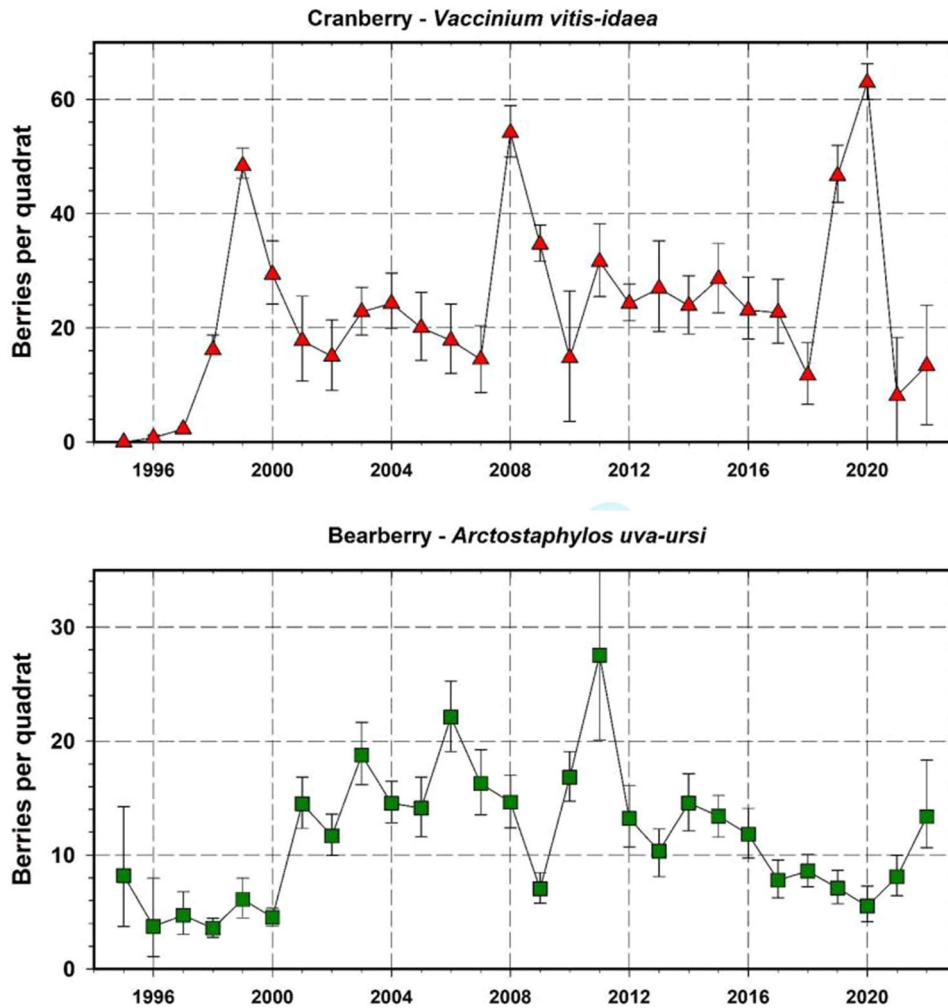


Figure 4 Average berry counts for two common species of ground berry (cranberry and bearberry) at Kluane Lake from 1995 to 2022. Quadrat size is 40 by 40 cm. An average of 700 quadrats were counted each year. Error bars are 95% confidence intervals. The correlation between these two time-series is 0.03.

as a weak indicator of good vegetation growing seasons (c.f. Supporting Information).

Climate is changing in the southern Yukon as it is everywhere in the north, but these changes in temperature and precipitation have had little effect on small mammals. The increase in peak density of our red-backed voles after 2000 might reflect increased primary production via changes in soil nutrients (Boonstra *et al.* 2017) or a shortened winter period since that time. Alternatively, it could reflect the disappearance in the forest of the arctic ground squirrel after 2000 (Werner *et al.* 2015), a generalist herbivore well known to prey on microtine rodents (Boonstra *et al.* 1990; McLean 2018). We have no data to test these two hypotheses.

1. Cyclic dynamics

There is an incongruence in Fig. 1 which shows a clear 3–4-year cycle in red-backed vole numbers since 1973 to the present, and our analyses of the 10 possible ecological variables on which we have data that show no cyclic tendency that would cause 3–4-year population changes. Fig. 4 illustrates the problem. The changes in cranberry and bearberry production, which are important contributors to summer rates of increase, do not show 3–4-year cycles over this time period. Fig. 5 illustrates the same problem for total berry production. Berry species are distributed patchily in Kluane forests, and these numbers are an index of berry production since we did not do random sampling but chose only quadrats

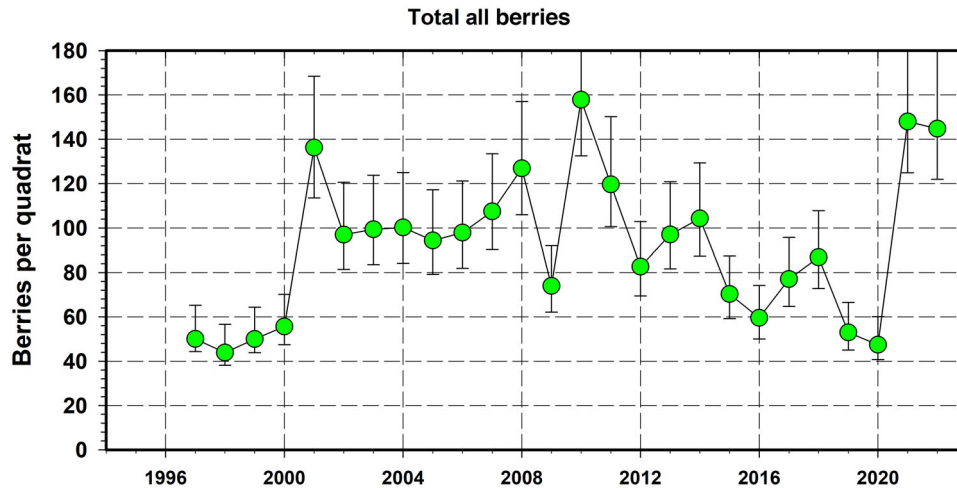


Figure 5 Average berry counts for all 5 common species of ground berries at Kluane Lake from 1995 to 2022. Quadrat size is 40 by 40 cm. Error bars are 95% confidence intervals. There is no indication of a clear 3–4-year cycle in berry counts that maps on to the 3–4-year red-backed vole cycle ($r = 0.08$, $n = 26$). There is a hint of a 10-year cycle but this requires 20 more years of data to validate.

that had at least 50% berry cover of one of the major species.

Something is clearly missing in our analysis, and the major demographic variable on which we have little data is social dynamics. Juvenile red-backed voles do not mature in their first summer except at very low population densities. Gilbert and Krebs (1981) showed by experimental addition of food that red-backed voles were limited in density by food supplies in summer but added food did not affect the length of the breeding season or increase the onset of juvenile maturity. Gilbert *et al.* (1986) experimentally reduced adult female red-backed voles and showed that juveniles released from competition from adult females would mature in their first summer of life in one year of high density (Fig. 6). The inference was that territorial females were responsible for a high rate of loss of young juveniles, before they reached a size that they could be live-trapped and ear tagged; we speculate that the loss could be due to infanticide among their neighbors or higher emigration rates immediately upon weaning. Bujalska (1973) suggested that spacing behavior was a strong component of the reasons reproductive output varied in populations of the bank vole (*Clethrionomys glareolus*). Saitoh (1981) found a similar pattern of reduced maturation in a high-density population of *Clethrionomys rufocanus*. Schweiger and Boutin (1995) fed populations of red-backed voles in winter at Kluane and reported increasing populations in winter on the fed grids, but a collapse in density in spring that was associated with the onset of breeding. Johnsen *et al.* (2017) fed bank vole

populations in Norway and showed that voles on fed grids had better overwinter survival than controls in one winter but not in another.

While food is clearly vital to overwinter populations under the snow, there are concerns that artificially fed populations attract more immigrants than control areas. We think this is the first analysis that attempts to measure the variability of natural food items in multiple winters and summers to determine its contribution to population changes. Our problem is that we have for our red-backed voles one year of measurement of the two interacting elements of social control—territoriality and reproductive inhibition. The conventional approach is to use density dependence as an aggregated variable to analyze population changes. Fig. 7 illustrates the density dependence relationships in our data from summer increases and winter declines. There is no sign of density dependence in summer, but a modest significant relationship in winter ($R^2 = 0.39$, $n = 48$ years). We do not know the exact causes of this winter density-dependence, and we do not suggest that all of it is due to social factors, but the type of detailed data illustrated by Krebs and Boonstra (1978) obtained in temperate *Microtus* populations showed that the largest amount of overwinter decline occurred in a few weeks at the start of breeding. These types of data are not easily obtained in these northern vole populations due to extensive snow cover and melt at this time of year when adults are starting to breed. Our suggestion is that the key lies in the social interactions that lead to reproductive inhibition in the peak summer (e.g. Mihok & Boonstra 1992),

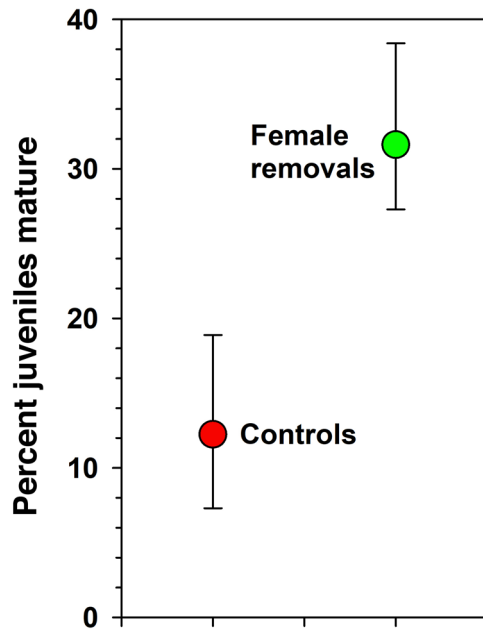


Figure 6 Juvenile maturation rates in the first summer of life for red-backed voles at Kluane Lake when adult females were removed early in the summer. Data from Gilbert & Krebs (1986, table 3). 95% confidence limits shown. This experiment suggests that juvenile maturation in the first summer of life is under social control.

which reduces viability via epigenetic changes in the offspring's brain function (Edwards *et al.* 2021; Huang *et al.* 2021a, 2021b). We do not have these kinds of data for our study.

The evidence is suggestive but inconclusive that the interactions associated with social behavior are necessary and sufficient to produce the cycles observed in these voles. We are left with more understanding on how food and winter weather contribute to population fluctuations but not knowing exactly what demographic mechanisms account for these 3–4-year cycles in red-backed voles at Kluane.

CONCLUSIONS

We have an extensive set of data that have led to a clearer understanding of the array of processes that have been postulated to cause population changes in these northern voles. In this paper, we have adopted a natural history approach to ask what ecological conclusions can be reached with data on food items, predators, and

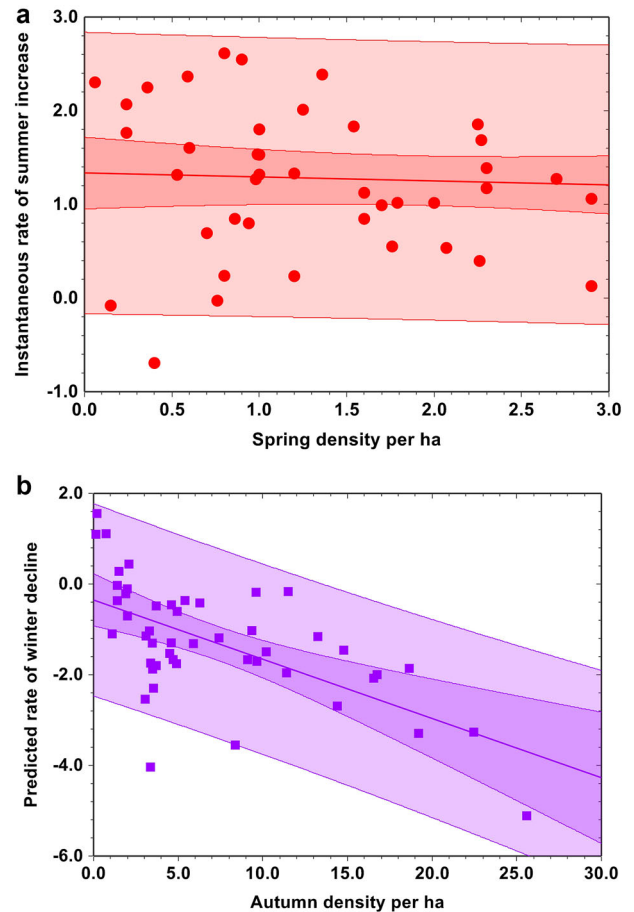


Figure 7 Density dependence in red-backed voles in summer and winter, Kluane Lake, all controls, 1974 to 2022, along with 95% confidence and prediction limits. Summer data, $r^2 = 0.01$, $n = 49$. Winter data, $r^2 = 0.39$, $n = 48$.

weather over a long time series, but even with a detailed description of changes in major food items, predation levels, and weather variation and how these factors correlate with summer gains and winter losses, we are left with the enigma that we have no clear model of what generates the consistent 3–4-year cycles in the populations of this rodent. We suggest that the answer could be in the details of social biology and epigenetic effects that will require more experimental study. In a similar vein that we see in trying to understand climate change, a combination of descriptive monitoring and analytical experiments are essential components of advancing our understanding of how ecological communities work.

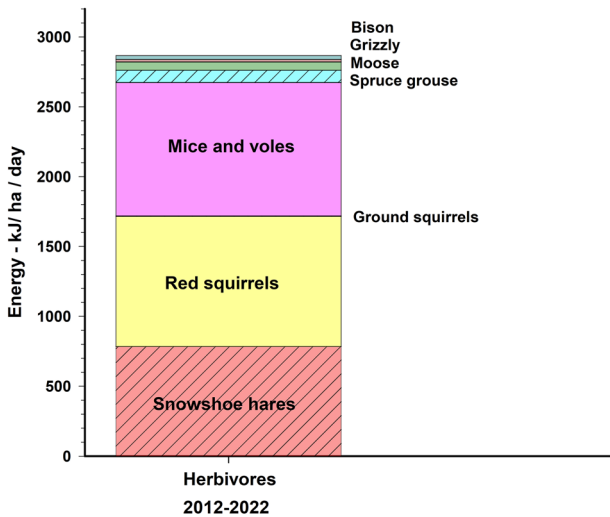


Figure 8 Average energy flow for the dominant herbivores in the Kluane ecosystem, 2012–2022. Mice and voles contribute more energy flow than all the large mammals combined and for this time period more even than snowshoe hares. Red-backed voles contribute 85% of the mice and vole group energy flow. Data for comparison are given in Krebs *et al.* (2019, fig. 2). Energy flow estimated from average density of each species and the equations in Nagy *et al.* (1999).

Fig. 8 provides a postscript to this paper in showing the contribution of the major vertebrates to the energy flow in the Kluane boreal forest ecosystem. The climate change signature is clearly shown in the recent large contribution of mice and voles to energy flow among the herbivores, in comparison with that shown in Krebs *et al.* (2019, fig. 2). The contribution to ecosystem energy flow is inversely related to the body size of the species, so red-backed voles and other mice although small and apparently insignificant to the human observer contribute about 30% of the herbivore energy flow.

ACKNOWLEDGMENTS

We thank the many students and summer assistants who have worked to gather these data over the past 50 years. We acknowledge the continued funding for this research from the Natural Sciences and Engineering Research Council of Canada and the vital support of the Arctic Institute of North America, in particular Andy, Carole, and Sian Williams, and the recent support of the Green Team funded by the Yukon Government to continue gathering these data.

REFERENCES

- Andreassen HP, Sundell J, Ecke F *et al.* (2021). Population cycles and outbreaks of small rodents: Ten essential questions we still need to solve. *Oecologia* **195**, 601–22.
- Arif S, MacNeil MA (2022). Predictive models aren't for causal inference. *Ecology Letters* **25**, 1741–5.
- Boonstra R, Andreassen HP, Boutin S *et al.* (2016). Why do the boreal forest ecosystems of Northwestern Europe differ from those of Western North America? *BioScience* **66**, 722–34.
- Boonstra R, Boutin S, Jung TS, Krebs CJ, Taylor S (2018). Impact of rewilding, species introductions and climate change on the structure and function of the Yukon boreal forest ecosystem. *Integrative Zoology* **13**, 123–38.
- Boonstra R, Krebs CJ (2012). Population dynamics of red-backed voles (*Myodes*) in North America. *Oecologia* **168**, 601–20.
- Boonstra R, Krebs CJ, Gilbert S, Schweiger S (2001). Chapter 10: Voles and mice. In: Krebs CJ, Boutin S, Boonstra R, eds. *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. Oxford University Press, New York, pp. 215–39.
- Boonstra R, Krebs CJ, Kanter M (1990). Arctic ground squirrel predation on collared lemmings. *Canadian Journal of Zoology* **68**, 757–60.
- Boonstra R, Krebs CJ (2006). Population limitation of the northern red-backed vole in the boreal forests of northern Canada. *Journal of Animal Ecology* **75**, 1269–84.
- Boonstra R, Krebs CJ, Cowcill K (2017). Responses of key understory plants in the boreal forests of western North America to natural versus anthropogenic nitrogen levels. *Forest Ecology and Management* **401**, 45–54.
- Boutin S, Krebs CJ, Boonstra R *et al.* (1995). Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* **74**, 69–80.
- Bujalska G (1973). The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility, Supplement* **19**, 465–74.
- Doyle FI, Smith JNM (2001). Raptors and scavengers. In: Krebs CJ, Boutin S, Boonstra R, eds. *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. Oxford University Press, New York, pp. 377–404.

- Edwards PD, Frenette-Ling C, Palme R, Boonstra R (2021). A mechanism for population self-regulation: social density suppresses GnRH expression and reduces reproductivity in voles. *Journal of Animal Ecology* **90**, 784–95.
- Fauteux D, Gauthier G, Berteaux D (2016). Top-down limitation of lemmings revealed by experimental reduction of predators. *Ecology* **97**, 3231–41.
- Gilbert BS, Krebs CJ (1981). Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia* **51**, 326–31.
- Gilbert BS, Krebs CJ (1991). Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon, 1973–1989. *Holarctic Ecology* **14**, 250–59.
- Gilbert BS, Krebs CJ, Talarico D, Cichowski DB (1986). Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology* **55**, 543–52.
- Huang S, Li G, Pan Y *et al.* (2021a). Population variation alters aggression-associated oxytocin and vasopressin expressions in brains of Brandt's voles in field conditions. *Frontiers in Zoology* **18**, 56.
- Huang S, Li G, Pan Y *et al.* (2021b). Density-induced social stress alters oxytocin and vasopressin activities in the brain of a small rodent species. *Integrative Zoology* **16**, 149–59.
- Hughes BB, Beas-Luna R, Barner A *et al.* (2017). Long-term studies contribute disproportionately to ecology and policy. *BioScience* **67**, 271–81.
- Johnsen K, Boonstra R, Boutin S, Devineau O, Krebs CJ, Andreassen HP (2017). Surviving winter: Food, but not habitat structure, prevents crashes in cyclic vole populations. *Ecology and Evolution* **7**, 115–24.
- Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005). Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society of London B* **272**, 193–202.
- Krebs CJ, Boonstra R (1978). Demographic attributes of the spring decline in populations of the vole *Microtus townsendii*. *Journal of Animal Ecology* **47**, 1007–15.
- Krebs CJ, Boonstra R (1984). Trappability estimates for mark-recapture data. *Canadian Journal of Zoology* **62**, 2440–44.
- Krebs CJ, Boonstra R, Cowcill K, Kenney AJ (2009). Climatic determinants of berry crops in the boreal forest of the southwestern Yukon. *Botany* **87**, 401–8.
- Krebs CJ, Boonstra R, Gilbert BS, Kenney AJ, Boutin S (2019). Impact of climate change on the small mammal community of the Yukon boreal forest. *Integrative Zoology* **14**, 528–41.
- Krebs CJ, Boutin S, Boonstra R (2001). *Ecosystem Dynamics of the Boreal Forest: the Kluane Project*. Oxford University Press, New York.
- Krebs CJ, Carrier P, Boutin S, Boonstra R, Hofer EJ (2008). Mushroom crops in relation to weather in the southwestern Yukon. *Botany* **86**, 1497–502.
- Krebs CJ, Wingate I (1976). Small mammal communities of the Kluane Region, Yukon Territory. *Canadian Field-Naturalist* **90**, 379–89.
- LaMontagne JM, Peters S, Boutin S (2005). A visual index for estimating cone production for individual white spruce trees. *Canadian Journal of Forest Research* **35**, 3020–26.
- Lindenmayer DB, Likens GE (2009). Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution* **24**, 482–86.
- Lindenmayer DB, Likens GE, Andersen A *et al.* (2012). Value of long-term ecological studies. *Austral Ecology* **37**, 745–57.
- McLean BS (2018). *Urocitellus parryii* (Rodentia: Sciuridae). *Mammalian Species* **50**, 84–99.
- Mihok S, Boonstra R (1992). Breeding performance in captivity of meadow voles (*Microtus pennsylvanicus*) from decline- and increase-phase populations. *Canadian Journal of Zoology* **70**, 1561–6.
- Nagy KA, Girard IA, Brown TK (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition* **19**, 247–77.
- O'Donoghue M, Slough BG, Poole K *et al.* (2022). Snow track counts for density estimation of mammalian predators in the boreal forest. *Wildlife Research* **50**, 425–34.
- Rohner C, Doyle FI, Smith JNM (2001). Great horned owls. In: Krebs CJ, Boutin S, Boonstra R, eds. *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. Oxford University Press, New York, pp. 339–76.
- Saitoh T (1981). Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology* **50**, 79–87.
- Schweiger S, Boutin S (1995). The effects of winter food addition on the population dynamics of *Clethrionomys rutilus*. *Canadian Journal of Zoology* **73**, 419–26.

Sinclair ARE (1998). Natural regulation of ecosystems in protected areas as ecological baselines. *Wildlife Society Bulletin* **26**, 399–409.

Werner JR, Krebs CJ, Donker SA, Boonstra R, Sheriff MJ (2015). Arctic ground squirrel population collapse in the boreal forests of the Southern Yukon. *Wildlife Research* **42**, 176–84.

Cite this article as:

Krebs CJ, Kenney AJ, Gilbert BS, Boonstra R (2024). Long-term monitoring of cycles in *Clethrionomys rutilus* in the Yukon boreal forest. *Integrative Zoology* **19**, 27–36. <https://doi.org/10.1111/1749-4877.12718>

SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Complete multiple regression analysis