

Population dynamics of red-backed voles (*Myodes*) in North America

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Abstract We review the population dynamics of red-backed voles (*Myodes* species) in North America, the main deciduous and coniferous forest-dwelling microtines on this continent, and compare and contrast their pattern with that of the same or similar species in Eurasia. We identify 7 long-term studies of population changes in *Myodes* in North America. Using autoregressive and spectral analysis, we found that only 2 of the 7 show 3- to 5-year cycles like those found in some Eurasian populations. There was no relationship between latitude and cycling. The general lack of cyclicity is associated with two key aspects of their demography that act in tandem: first, poor overwinter survival in most years; second, chronically low densities, with irregular outbreak years. Eight factors might explain why some *Myodes* populations fluctuate in cycles and others fluctuate irregularly, and we review the evidence for each factor: food supplies, nutrients, predation, interspecific competition, disease, weather, spacing behavior and interactive effects. Of these eight, only food supplies appear to be sufficient to explain the differences between cyclic and non-cyclic populations. Irregular fluctuations are the result of pulsed food supplies in the form of berry crops (*M. rutilus*) or

tree seeds (*M. gapperi*) linked to weather patterns. We argue that, to understand the cause for the patterns in the respective hemispheres, we must know the mechanism(s) driving population change and this must be linked to rigorous field tests. We suggest that a large-scale, year-round feeding experiment should improve overwintering survival, increase standing densities, and flip non-cyclic *Myodes* populations into cyclic dynamics that would mimic the patterns seen in the cyclic populations found in parts of Eurasia.

Keywords Population regulation · Population cycles · *Myodes* · Winter weather · Food shortage · Population limitation

Introduction

Red-backed voles are a major component of the small rodent community in the boreal and deciduous forests of North America. Though many demographic studies have been carried out on these voles in North America during the last 50 years, no one has brought these studies together to obtain a continent-wide evaluation of the patterns of population change. The literature on small rodents in the northern hemisphere has often focused on the importance of cyclic fluctuations, following the lead of Elton's classic book (1942) (for more recent summaries of the status of the field, see reviews by Krebs and Myers 1974; Taitt and Krebs 1985; Krebs 1996; Stenseth 1999; Korpimäki et al. 2004). The underlying theoretical problem being addressed is one of the central problems in ecology, that of population regulation and the density-dependent processes operating to bring populations back to equilibrium density (Sinclair 1989; Krebs 1995). A second theme that has pervaded the literature on rodent population cycles is that cycles are

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more common as one moves north and that the intensity of population fluctuations also increases toward the north (Hansson and Henttonen 1985a; Bjørnstad et al. 1995). Unlike the study of the North American *Microtus* voles and lemmings, the study of red-backed voles on this continent has made little contribution here as they do not seem to cycle nor show latitudinal gradients, with densities generally being low and often fluctuating in irregular ways (note that previous papers have referred to this genus as *Clethrionomys*, but it has now been revised to *Myodes*; Carleton et al. 2003). However, the study of their dynamics has been directly related to a second major problem in population ecology—what are the factors that limit numbers, setting equilibrium density, and thus affecting population growth (Krebs 2002)?

Here, we review all long-term and short-term studies of *Myodes* populations that have been carried out in Canada and the United States with a view to answering three questions:

- (1) Do *Myodes* populations in North America show 3- to 5-year cyclic fluctuations?
- (2) What mechanistic factors are responsible for population changes in North American *Myodes*?
- (3) How do the population patterns found in North American *Myodes* compare with those of the same or similar species in Eurasia?

We also examine short-term studies, some of which were primarily demographic in nature and some of which were experimental, to obtain a comprehensive picture of the range of variation found across the continent and to provide insight into the underlying mechanisms limiting numbers and thus driving demographic changes.

Geographical distributions

Three species of *Myodes* are found in North America (Fig. 1). The northern red-backed vole (*M. rutilus*) has a

holarctic distribution. It appears to be a post-glacial colonizer of North America, with close genetic relationships existing between North American and Far Eastern Siberian populations (Cook et al. 2004). In North America, it occurs north of latitude 60°N in the boreal forest and tundra regions (Banfield 1974). In the tundra, it is limited to southern areas and does not occur on the arctic islands of Canada. The southern red-backed vole (*M. gapperi*) is endemic to North America occurring approximately south of 60°N latitude across Canada. In the United States, it occurs in the forests across the north, with its range extending down along the mountain ranges on both sides of the continent: in the west down the Rocky Mountains to southwestern New Mexico and Arizona and in the east down the Appalachians to northern Georgia (Merritt 1981). This species is closely related to, and nearly indistinguishable from, *M. glareolus* of Eurasia (Cook et al. 2004), with which it will interbreed successfully, producing F₁s but not F₂s (Grant 1974). The western red-backed vole (*M. californicus*) is endemic to North America, being found only in western Oregon and northern California (Alexander and Verts 1992).

The distribution of these three species in North America is entirely parapatric, so that there is never the overlap found in Fennoscandia, where up to 3 species can occur together (Henttonen et al. 1977; Stenseth 1985; note that we will not discuss *M. rufocanus* as there is no counterpart in North America). The parapatric distributions found in North America are most strikingly illustrated in the studies by Fuller (1969) from the Northwest Territories (NWT) in which *M. rutilus* occupied one side of a river and *M. gapperi* the opposite bank with no overlap. What prevents overlap between these two species is not known (McPhee 1977). Other small mammal species do co-occur with *Myodes* in North America. Over most of *Myodes* range, deermice (*Peromyscus* spp.) occur in the same habitats. In eastern North America, the woodland jumping mouse (*Napaeozapus insignis*) occupies the same habitats

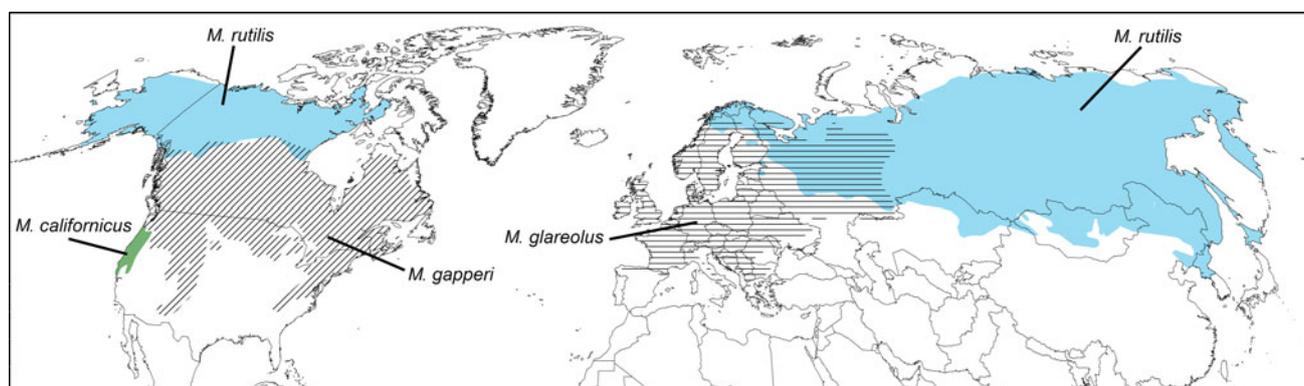


Fig. 1 Geographical distribution of the major species of *Myodes* in North America and Eurasia

as *M. gapperi* (Whitaker and Wrigley 1972; Vickery 1981). Several *Microtus* species as well as heather voles (*Phenacomys* spp.) can also be found in the same habitats as *Myodes* spp. in the southern Yukon (Krebs and Wingate 1976), Northwest Territories (Mihok 1979), and Manitoba (Turner et al. 1975).

Natural history

Critical to understanding the population dynamics of these species is knowledge of their basic biology and the constraints of diet and habitat. They are short-lived, with a maximum lifespan of about 1 year, and, as a result, their entire breeding lifespan is compressed into one season. Females have a high reproductive rate, with gestation period of 17–19 days, 5–6 young per litter (though <3 in *M. californicus*), and postpartum estrus; thus, they are both pregnant and lactating for much of the breeding season (Alexander and Verts 1992; Merritt 1981; Innes and Millar 1994). The length of the breeding season varies with latitude: in *M. rutilus* being about 4–5 months (May–September—the snow-free period; Gilbert and Krebs 1981), though evidence for very occasional winter breeding has been documented (Fuller 1969; West 1982); in *M. gapperi* being 5 months in the NWT (Mihok 1979) to 8 months in Colorado (late winter to late Fall; Merritt 1981); and in *M. californicus* being up to 9 months (Alexander and Verts 1992).

Diet and habitat are key variables in their population dynamics: *M. californicus* is the most specialized, *M. rutilus* is moderately specialized, and *M. gapperi* is the least specialized. Though it has been captured in a variety of habitats in the Pacific Northwest, *M. californicus* is primarily a species of the closed-canopy, cool, moist old-growth coniferous forests with little undergrowth (trees such as redwood *Sequoia sempervirens*, Sitka spruce *Picea sitchensis*, and Douglas fir *Pseudotsuga menziesii*, Alexander and Verts 1992). Clearcutting virtually eliminates them (Gashwiler 1970). Their diet throughout the year consists primarily of the sporocarps of mycorrhizal hypogeous fungi (Maser et al. 1978), and the abundance of these is linked to the high moisture levels found in mature forests (Slankis 1974). Movement patterns are closely associated with decaying logs (Tallmon and Mills 1994), and these may serve as source of the fungi during the drier periods of the year.

The habitat of *M. rutilus* is largely restricted to the coniferous forests dominated by black and white spruce (*P. mariana* and *P. glauca*) and to those areas recovering from forest fires (Fuller 1969; Whitney 1976; West 1982). In the southern Yukon, we virtually never caught them in grassland habitat (Boonstra and Krebs 2006). It eats a wide variety of foods (Dyke 1971; Grodzinski 1971; West 1982), including seeds of dwarf shrubs (e.g., *Arctostaphylos* spp., *Empetrum nigrum*, *Vaccinium* spp.), leaves of

herbs, shrubs, and trees, lichens, epigeous and hypogeous fungi, and occasionally mosses and arthropods. Fungi are eaten only in summer when they are abundant (Krebs et al. 2008). Though it will eat spruce seeds, it cannot survive on them (Grodzinski 1971) and nor do populations increase in spruce mast years (Boonstra and Krebs 2006). Seeds from the dwarf shrubs appear to be key to vole overwinter survival and population growth (Dyke 1971; West 1982; Krebs et al. 2010).

Both the habitat and diet of *M. gapperi* are the broadest of the three species. It has a relatively high moisture requirement (Getz 1968) and is thus primarily found in mesic habitats in coniferous, deciduous, and mixed forests with abundant litter (Merritt 1981; Nordyke and Buskirk 1991; Morris 1996). Its diet is omnivorous and opportunistic, changing with season and availability, consisting of dicotyledous leaves in Spring and late Fall, seeds, berries, fruits, and insects during the summer and Fall, and monocots, mosses, and lichens throughout the year (Perrin 1979a; Merritt and Merritt 1978; Martell 1981; Merritt 1981; Vickery 1979). Fungi are also consumed in summer when available and may be a dominant food item when abundant (Merritt and Merritt 1978; Martell 1981), but these may disappear from the diet during dry years (Ovaska and Herman 1986). Though an initial analysis of the first 10 years of data from Maine showed no response of *M. gapperi* populations to mast years of red oak, red maple, or white pine (McCracken et al. 1999), a longer 22-year time series (Elias et al. 2006) found a positive relationship to white pine seed crops. In a 3-year study in Connecticut, populations were positively correlated to red maple seed crops (Schnurr et al. 2002). Clear-cutting and forest fires caused a marked decline in the populations of this vole, possibly because of competition with *Peromyscus* spp. (Martell 1983a; Gliwicz and Glowacka 2000; Klenner and Sullivan 2003; Sullivan et al. 2008).

Materials and methods

We examined all the available data on population changes in North American *Myodes* and included data from both live-trap and snap-trap studies. Density estimates come only from live-trapping studies. We have tried where possible to standardize the estimates to approximate density per hectare by adding a boundary strip to live-trapping studies, following the recommendations of Bondrup-Nielsen (1983). The intensity of trapping was often significantly less than that from North American studies on *Microtus* spp. (i.e. twice a season vs. biweekly trapping sessions) and hence the shorter time-scale changes in demography are missing (exactly when increases or declines occurred relative to reproduction and seasonal

changes: e.g., did overwinter declines occur during the winter, nonbreeding season or at the onset of the breeding season in Spring). This will affect our ability to elucidate the causal mechanisms of population change (Krebs and Boonstra 1978). However, in general, the intensity of data collection was similar to that obtained on *Myodes* studies in Eurasia. The statement of Cheveau et al. (2004) that studies of small mammal population dynamics in these forests are fragmentary is without foundation. To obtain accurate density estimates, we pursued one of two approaches: either we contacted the investigator directly to obtain the original data or we scanned the published population graphs, saved them as a PICT file, and read the data points with the program DATATHIEF (<http://www.datathief.org>; copyrighted by K. Huyser and J. van der Laan, Computer Systems Group, Nuclear Physics Section, National Institute for Nuclear Physics and High Energy Physics, Amsterdam, The Netherlands).

To obtain comparative measures of population change in the three species, we calculated two indices (summer growth and overwinter survival) using live-trap data, snap-trap data, or both. Summer population growth was the Fall estimate (t)/Spring estimate (t) and winter population decline was the Spring estimate ($t + 1$)/Fall estimate (t). One caveat that has to be borne in mind is that, when grid sizes are small relative to the home ranges of the voles or when population densities are low (Boonstra and Krebs 2006), population indices become increasingly unreliable and the ability to detect population increases from declines may be limited.

To summarize the variation in population abundance over time, we calculated the s index (standard deviation of log-10 abundance) for all studies that had at least 5 years of data collected in a standardized way. Included are both live-trapping and snap-trapping studies. Spring and late summer s indices were calculated separately. This index has been heavily used for the Fennoscandian *Myodes* species, with only populations with an s index >0.5 being regarded as exhibiting the 3- to 5-year cycle (Hansson and Henttonen 1985b; Henttonen et al. 1985). This definition of a cycle is not valid because the s index measures only population variability and does not separate cyclic and non-cyclic population changes (McArdle and Gaston 1992). To achieve a precise mathematical definition of cycling we need to use autoregressive modeling and spectral analysis.

Autoregressive modeling and spectral analysis

We analyzed all the time series data on North American populations that had at least 14 years of consecutive estimates. We used late summer or Fall estimates in preference to Spring estimates but the same results were found with

each when both were available. We used Statistica 6.0 to analyze time series by calculating autocorrelation coefficients and by fitting autoregressive models of order 2 to the data. Following Bjørnstad et al. (1995), we log-transformed population estimates and fitted the autoregressive model:

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

where $R_t = X_t - X_{t-1} = \log(N_t/N_{t-1})$; $X_t = \log(N_t)$; N_t = abundance estimate for year t ; t = time in years. 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 in Statistica 6.0 after detrending the data, and smoothed the resulting periodogram with a 5-point moving average based on Hamming weights.

Results

Demographic patterns

The overall pattern of demographic change in North America for all long-term population studies of *M. rutilus* can be seen in Fig. 2 and for representative long-term studies of *M. gapperi* in Fig. 3. For the latter species, one recent long-term study from Maine (Elias et al. 2006) presents a published graph of population change in late summer, but we were able to get Spring data for this population as well from the authors. In *M. rutilus*, the basic pattern is one of summer growth and winter decline. Only the Yukon population shows any evidence of a 3- to 5-year cycle, whereas population changes in Alaska and the NWT appear largely annual, with populations occasionally reaching densities 2–3 times their typical summer levels, but with no obvious pattern. The detailed Alaskan studies, with multiple trapping sessions in summer and, in some years, also in winters, indicate that population declines typically occur during the winter (e.g. Fig. 2c, 1973) but not always (Fig. 2c, 1976; see also NWT Fig. 2b, 1966 and 1967).

The general pattern of demographic change from representative population studies in Eurasia can be seen for *M. rutilus* in Fig. 4 and for *M. glareolus* in Fig. 5. In *M. rutilus*, good evidence for cycling can be seen at both the Finnish sites (Fig. 4a, c) and at the adjacent Kola Peninsula site in Russia, (Fig. 4d), but not in the central portion of the Eurasia (southern Siberia) where population changes are only annual. In *M. glareolus*, cycling can again be seen at the Finnish (Fig. 5c) and Czech (Fig. 5d) sites, but not at either the Polish (Fig. 5a) or English (Fig. 5b) sites. Thus, as has been highlighted by Henttonen et al. (1985, 2000),

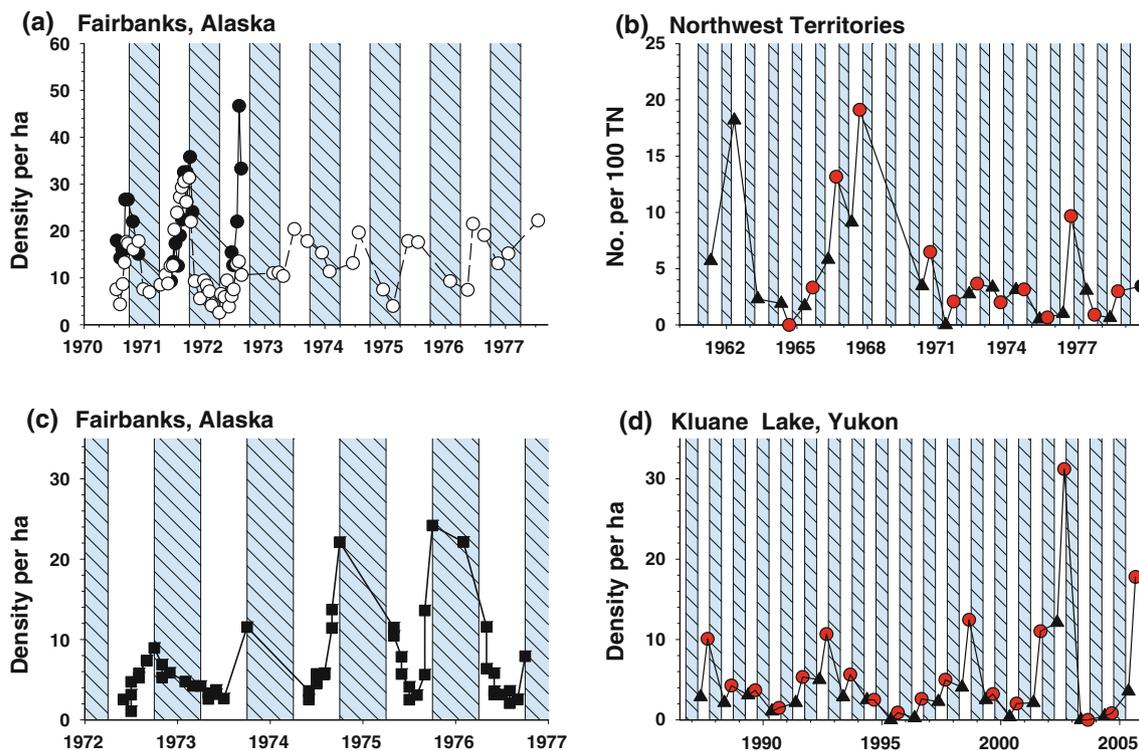


Fig. 2 Population density changes in *Myodes rutilus* from North America. Winter months are shaded. **a** Whitney and Feist (1984) data from two live-trapping grids near Fairbanks, Alaska. **b** Fuller (1977) snap-trap data from Heart Lake, NWT Canada. **c** West (1982) data

Korpimäki et al. (2005) and others, there is strong evidence of cycling only in some regions of Eurasia.

We summarize the mean densities for the North American studies in Spring and Fall and summer growth and winter decline in Table 1. In three of the studies, Spring densities are low (mean 1.3–2.6/ha) whereas an apparently more productive site in Alaska had 3–9 times higher Spring densities. However, these latter densities are severe overestimates because of the small size of the trapping grids (0.2 ha) with large edge effects, with no individual vole having its entire home range encompassed by the grid. Even West's (1982) grid size of 0.77 ha in Alaska, Fuller's (1977) of 2.25 ha in the NWT) (see comments in Fuller 1985a), and, at times, Boonstra and Krebs' (2006) of 2.81 ha in the Yukon were too small. In three of the studies, densities increase 3 times from Spring to summer whereas in the other Alaskan site densities increase over 6 times. Oddly, these four studies show the full range of overwinter loss, with one Alaskan population dropping about 80% virtually every winter, but the NWT (snap-trapped populations only) and the Yukon population (only live-traps were used) showing little loss. As well at the NWT site, the picture of population change differs depending on the trap type used: that from live-traps indicates both greater summer growth and greater winter

loss than that shown by the snap-traps. However, the number of years from the live-trap study is low. In *M. gapperi*, Spring densities in all but one population (Colorado) were <4/ha (range of means 0.73–3.71; Table 1) whereas mean Fall densities are 2–9 times that (range of means 1.92–14.49/ha). Most studies show populations increasing by at least 3 times over the summer with at least three increasing 6–9 times. Overwinter losses cause populations to decline by 25–35% in five studies, 30–50% in three others, and 0% in one (NWT). The latter again highlights the different pictures resulting from snap-trap data (no overwinter loss) versus live-trap data (loss of 70%).

In *M. californicus*, we only have one study with population data on an unlogged site. We have no estimates of home range and thus have not corrected densities as with the other species, calculating them based on the size of the grid and one trap interval around the perimeter. This species appears remarkably stable over time. Densities are generally low in both Spring and Fall (3.5–4.5/ha; Table 1), with populations growing modestly in summer (about 2 times) and then similarly declining little over winter (only about 15%).

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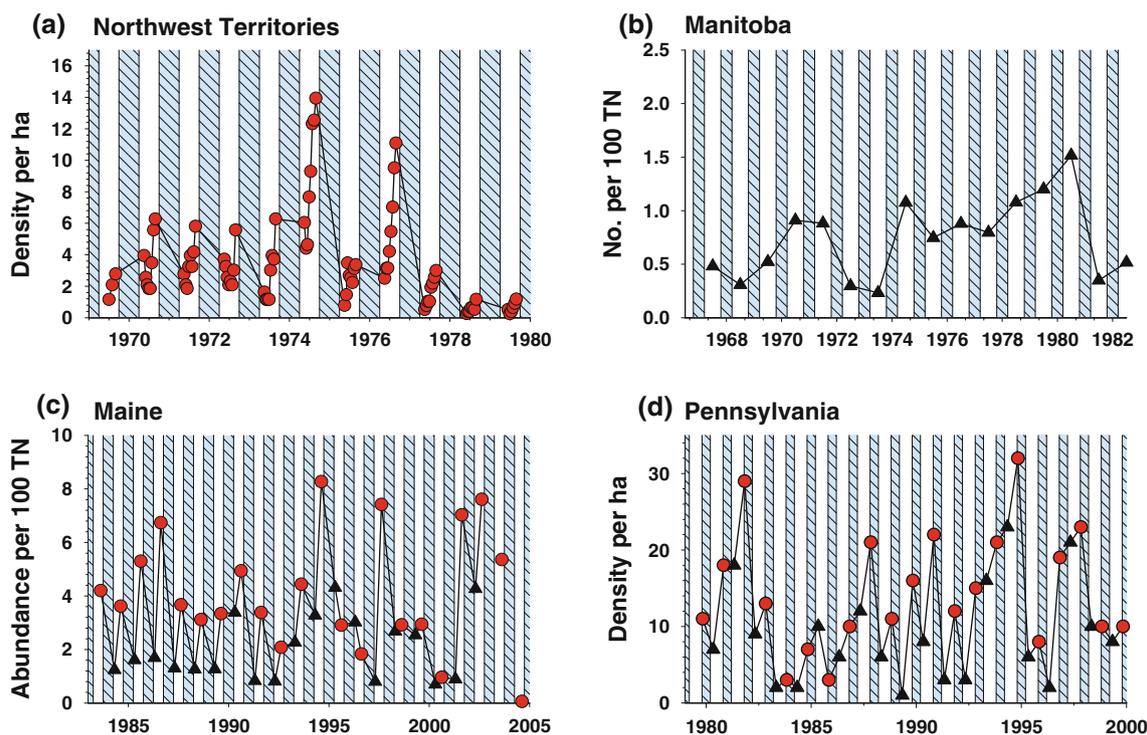


Fig. 3 Population density changes in *Myodes gapperi* from North America. Winter months are shaded. **a** Fuller (1977) live-trap data from Heart Lake, NWT, Canada. **b** Mihok et al. (1985a) snap-trap data from southern Manitoba, Canada. **c** Elias et al. (2006) data from

live-trapping in Maine, USA. **d** Merritt et al. (2001) and Merritt (personal communication) from south-western Pennsylvania. All live-trap data are corrected for effective grid size, following Bondrup-Nielsen (1983). For (c) and (d), triangles Spring data, circles Fall data

North American species have an index >0.5 in either Spring or Fall and thus do not meet the critical cutoff by this definition of a highly fluctuating population (Table 2). In *M. rutilus*, the higher latitude Alaskan populations are much less variable (s index range 0.04–0.22) than the slightly lower latitude populations in the NWT and Yukon (range 0.39–0.43). The ranges of variability are similar in *M. gapperi* (0.29–0.44) and *M. californicus* (0.32–0.43) and again, for the former, there is no relationship to latitude (for Fall: $r = 0.40$, $F_{1,4} = 0.50$, $P = 0.50$). In contrast, though none of our representative Eurasian *M. rutilus* populations have an index >0.5 , some of the *M. glareolus* populations do, though the relationship to latitude is not marked (for Fall: $r = 0.54$, $F_{1,4} = 1.20$, $P = 0.35$), with high indices occurring at both high and low latitudes.

Autoregressive modeling and spectral analysis

We analyzed all the *Myodes* population time series from North America that had a minimum of 14 years of data with the time series methods of autocorrelation, autoregressive modeling, and spectral analysis to determine if there was evidence of 3–4 year cycles in numbers and if so whether an autoregressive model of order 2 would fit the data. We appreciate that all but two of these time series

have a small sample size, and it is desirable to have a sample of 25 data points to produce a robust autoregressive model. For the time series of shorter duration, we think the models are indicative rather than precise.

The first indication of cyclic dynamics can be obtained from autocorrelation analyses. Table 3 gives the lag 1–5 autocorrelation coefficients for six populations of *M. gapperi* and one population of *M. rutilus*. For a cyclic population, the ideal configuration would be to have a positive autocorrelation at lag 1 year and negative autocorrelations at lag 2–4 years, suggesting a 3- to 5-year cycle in numbers. Only two time series showed significant lag 2 correlations—the Maine data for *M. gapperi* and the Kluane data for *M. rutilus*.

The second indication of cyclic dynamics can be obtained from autoregressive analyses. There were only two time series for North American populations that had a statistically significant second-order autoregressive model—the Maine data and the Kluane data (Table 4). Almost all the others had significant first-order regressions indicating some direct density dependence in the annual data. The positions of all the populations in phase space can be seen most easily on the periodicity diagram developed by Royama (1992). Figure 6 shows that the Maine, Yukon, and Minnesota populations Fall in the zone of

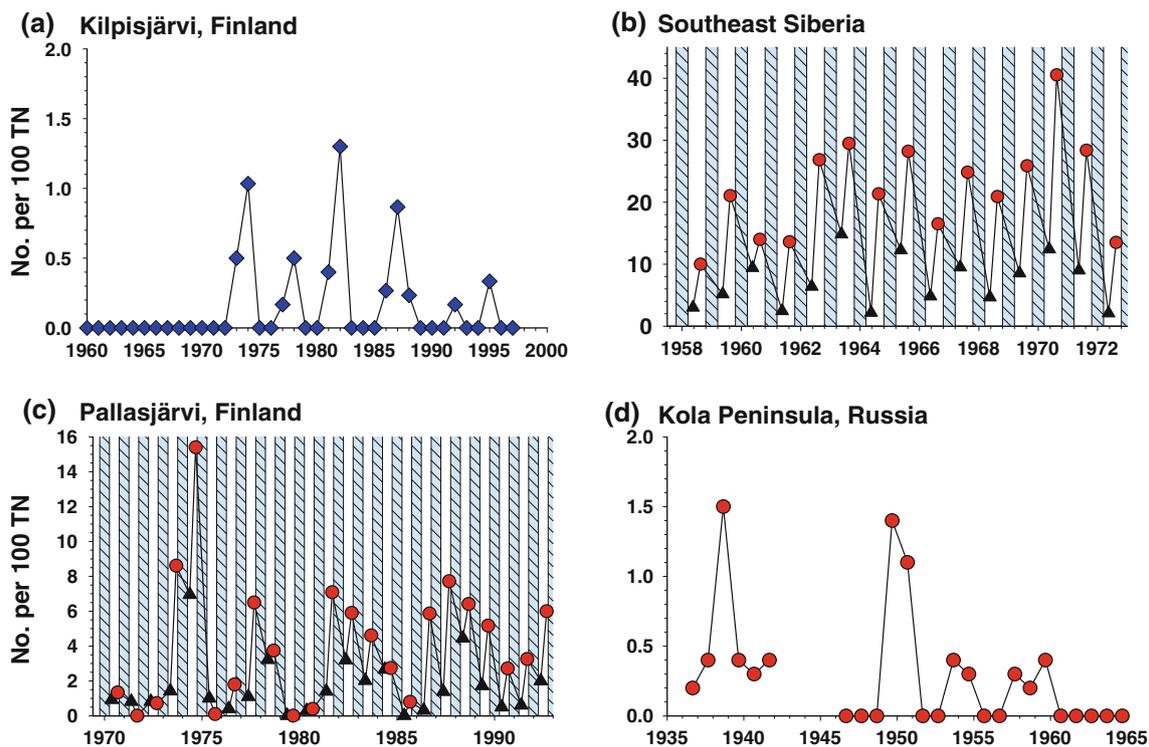


Fig. 4 Population density changes in *Myodes rutilus* from Eurasia. Winter months are shaded. **a** Kilpisjärvi, Finland snap-trap data from Henttonen (personal communication). **b** Koshkina and Korotkov (1975) snap-trap data from the Salair Foothills of Siberia.

c Pallasjärvi, Finland snap-trap data from Henttonen (personal communication). **d** Kola Peninsula, Russia snap-trap data from Koshkina (1966). For **(b)** and **(c)**, triangles Spring data, circles Fall data

expected 3- to 4-year cycles, whereas the other populations align on a gradient from possibly cyclic around 4–5 years (Manitoba) to borderline populations that could fluctuate at longer time periods than 4 years (NWT and Pennsylvania) to expected stability (Ontario).

Spectral analyses of the population indices supported the suggestion that clear evidence of 3- to 4-year fluctuations could be found in only 2 time series (Fig. 7). The Algonquin time series in particular shows no indication of any periodicity in the range of 2–5 years. Both the Minnesota and the Manitoba time series show a spectral peak in the 3- to 5-year range, but they are based on a small number of years of trapping.

Discussion

The population dynamics of these three forest dwelling voles span the gamut from irregular fluctuations at low density to evidence of cycles with a 3- to 5-year periodicity (Tables 2, 3 and 4), with all populations existing most of the time at low density. Within a species, populations living at approximately the same latitude may show both types of dynamics (e.g., *M. rutilus* populations in Alaska

are not cyclic whereas those in the southern Yukon may be; *M. gapperi* populations in southern Manitoba and central Ontario are not cyclic whereas those in Maine are) (Fig. 7). Neither of the two cyclic populations shown by the auto-correlation (Table 3) and autoregressive (Table 4) methods pass the 0.5 *s* index criterion for large fluctuations (Table 2). We dissect the nature of these differences to try to understand the factors or their interactions that may be responsible. The critical characteristic that limits some of these factors from playing a significant regulatory role is the low density and poor overwinter survival most of the time (Table 1). Below we discuss one at a time the plausible factors that could limit or regulate *Myodes* populations in North America, by first examining extrinsic factors, then examining an intrinsic factor, i.e. social factors, and finally, examining interactions between these factors. Although we will relate our findings to *Myodes* studies done in Eurasia, our primary purpose is to do a comprehensive overview of studies done in North America.

There is one key difference between the demography of the *Myodes* populations in Fennoscandia that cycle and those in North America that do not that may indicate the factor(s) responsible for the difference cycling and non-cycling. In Fennoscandia, breeding season declines are

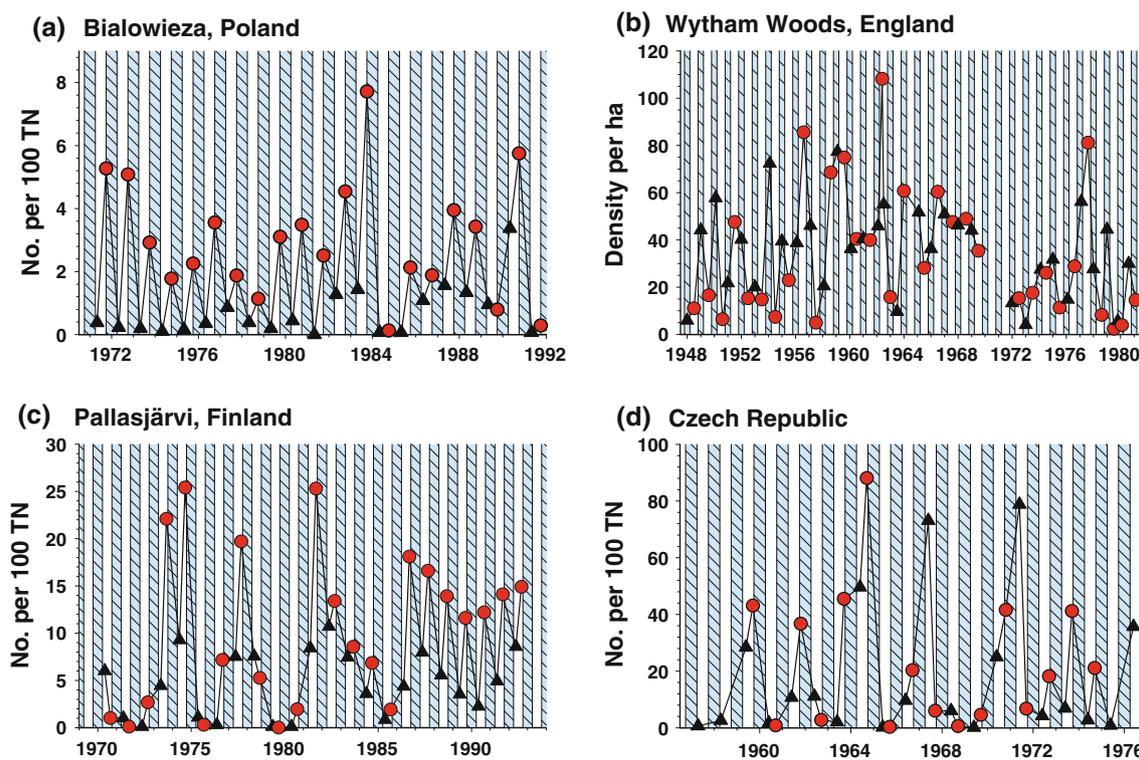


Fig. 5 Population density changes in *Myodes glareolus* from Eurasia. Winter months are shaded. **a** Bialowieza Forest, Poland, snap-trap data from Pucek et al. (1993). **b** Wytham Woods, England, live-trapping data from Southern and Lowe (1982). **c** Pallasjärvi, Finland

snap-trap data from Henttonen (unpublished data). **d** Czech Republic snap-trap data from Tkadlec and Zejda (1998a, b). Triangles Spring data, circles Fall data

common (e.g., Henttonen et al. 1987; Korpimäki et al. 1991; Norrdahl and Korpimäki 2000). However, in North America, breeding season declines seldom occur (e.g., West 1982; Fuller 1977; Bondrup-Nielsen 1987; Boonstra and Krebs 2006).

The other thing to be considered is that many of the long-term datasets rely on only one or two population estimates per year. These have a number of inherent problems and limitations that need to be acknowledged when trying to understand the cause(s) of population change. If population change happens rapidly (rather than gradually), such as sometimes occurs at the onset of winter without adequate snow cover or in Spring with the social reorganization that accompanies the onset of the breeding season, one may not be able to distinguish change attributable to winter mortality (Hansen et al. 1999) from that which is largely result of socially induced mortality in Spring (Krebs and Boonstra 1978). Most studies rely on only two population assessments per year—in Spring after snowmelt and in late summer or early Fall before winter sets in. At these two ends, if reproduction starts before the first, or ends after the second, then one may have missed population changes attributable to winter conditions or to Spring and summer conditions, respectively.

Food

Only two of the long-term time series show clear evidence of cyclic dynamics (*M. gapperi* in Maine and *M. rutilus* in the Yukon; Table 3), and spectral analysis in the former species suggest that populations from Manitoba and Minnesota show some evidence of cyclicity. The most parsimonious explanation for both cyclic and noncyclic vole population dynamics is the bottom-up explanation related to either periodic fluctuations in their food in the case of the former and insufficient food most of the time in the case of the latter (White 2008). This explanation presupposes that one knows what the key natural food(s) are and this has not been obvious until recently.

Two approaches have used to examine the food hypothesis: either manipulate it directly or correlate changes in food abundance with that in vole abundance. Feeding experiments have been attempted only on *M. rutilus*—three in North America (Gilbert and Krebs 1981; Schweiger and Boutin 1995; Boonstra and Krebs 2006) and one in Finland (Henttonen et al. 1987). The experiment of Boonstra and Krebs (2006) had no effect because the food (rabbit pellets) was inappropriate. The experiment of Henttonen et al. (1987) produced only marginal density

Table 1 Indices of population demography of *Myodes* spp. from North America from both short- and long-term studies

	Spring density			Fall density			Population change			
	$X \pm SE$	Range	<i>n</i>	$X \pm SE$	Range	<i>n</i>	Spring–Fall	<i>n</i>	Fall–Spring	<i>n</i>
<i>Myodes rutilus</i>										
Alaska ^a	2.38 ± 0.35	1.07–3.15	5	14.94 ± 3.42	7.91–24.19	5	6.67 ± 1.39	5	0.19 ± 0.04	4
Alaska ^b	11.55 ± 1.31	5.90–17.93	11	24.31 ± 2.87	13.50–46.69	11	3.19 ± 1.1	11	0.43 ± 0.07	9
NWT ^c	1.29 ± 0.26	0.78–1.55	3	15.72 ± 6.26	6.98–40.60	5	15.71 ± 6.26	3	0.13 ± 0.06	3
NWT ^d							2.47 ± 0.80	11	0.99 ± 0.19	9
Yukon ^e	2.03 ± 0.38	0–12.1	22	6.86 ± 1.41	0–31.2	22	3.66 ± 0.50	22	0.47 ± 0.10	20
<i>Myodes gapperi</i>										
NWT ^f	1.58 ± 0.41	0–5	15	5.29 ± 1.13	0–13.9	15	3.58 ± 0.46	13	0.29 ± 0.07	13
NWT ^g							2.82 ± 0.69	15	0.98 ± 0.25	14
Alberta ^h (coniferous)	0.73 ± 0.23	0.17–1.28	4	3.51 ± 0.72	1.62–4.98	4	6.12 ± 1.5	4	0.28 ± 0.11	2
Alberta ^h (deciduous)	2.61 ± 0.93	1.33–5.36	4	14.49 ± 3.37	8.60–22.32	4	9.44 ± 2.0	4	0.22 ± 0.02	2
Ontario ⁱ	1.37 ± 0.65	0.49–2.64	3	1.92 ± 0.71	0.49–2.64	3	2.28 ± 1.53	3	0.69 ± 0.31	3
Ontario ^j							8.54 ± 1.17	35	0.36 ± 0.09	35
Connecticut ^k	3.40 ± 0.58	2.55–4.5	3	11.30 ± 0.91	10.02–13.06	3	3.49 ± 1.03	3	0.25 ± 0.10	3
Colorado ^l	7.17 ± 1.24	5.93–8.4	2	28.71		1	4.0	1	0.29	1
Maine ^m							2.84 ± 0.55	19	0.54 ± 0.07	19
Pennsylvania ⁿ	3.71 ± 0.65	0.43–9.84	19	6.50 ± 0.76	1.28–13.69	20	3.04 ± 0.82	28	0.68 ± 0.12	12
<i>Myodes californicus</i>										
Oregon ^o	3.42 ± 0.74	0.60–8.37	11	4.53 ± 1.07	0.00–9.57	12	2.16 ± 0.76	9	0.85 ± 0.15	9

Population density estimates (no. per ha) come only from live-trapping studies and those of population change (summer growth [Fall estimate (*t*)/Spring estimate (*t*)] and overwinter loss [Spring estimate (*t* + 1)/Fall estimate (*t*)] come from studies using live-trapping or snap-trapping or both. *n* the number of years on which the study is based

^a West (1982), ^b Whitney and Feist (1984), ^c Fuller (1985a), live-trapped data from his Fig. 12, ^d Fuller (1985a), snap-trapped data from his Table 1, ^e Boonstra and Krebs (2006), ^f Fuller, live-trapped data collated from (1969, 1977), and (1985a, b), ^g Fuller (1977), snap-trapped data from his Fig. 2, ^h Bondrup-Nielsen (1987), ⁱ Martell (1983b), ^j Falls and Falls, unpublished data, ^k Miller and Getz (1977), ^l Merritt and Merritt (1978), ^m Elias et al. (2006) and Elias, Witham, and Hunter, unpublished data, ⁿ Merritt et al. (2001) and Merritt, unpublished data, ^o Gashwiler (1970)

effects because of the food (oats) was also not suitable. In addition, all five microtines species (including three *Myodes*) were pooled and thus the actual impact on *M. rutilus* could not be teased out. Gilbert and Krebs (1981) found that adding high quality food in summer (sunflower seeds had a positive effect, oats did not) increased the size of the Fall population by up to three times (partly through immigration, but also due to improved on-site juvenile survival). They concluded that natural summer food levels must constrain population growth (especially through early juvenile survival). Clearly, the food added was unnatural, but this study does indicate the demographic potential of this species that is sometimes realized under natural conditions (Fig. 2). Critical in unraveling the driver of density changes in this species is the observation that population density in Spring is a good predictor of that in the Fall (i.e. Springs with high density are correlated with Falls of high density) (Gilbert and Krebs 1981; Boonstra and Krebs 2006; Krebs et al. 2010). Thus, the conditions sustaining summer population growth must have already been present in Spring. In addition, Gilbert and Krebs (1981) found that

production of higher densities in the Fall did not carry over to the next Spring and thus some aspect of winter conditions must also constrain population change. Schweiger and Boutin (1995) tested this idea by adding food (sunflower seeds) during the Fall and winter and produced higher Spring densities. However, when they stopped feeding the next Spring, these higher Spring densities did not result in higher Fall densities. Thus, whatever food normally permits good overwintering survival and higher Spring density must carryover throughout the next summer. For *M. rutilus*, the critical natural food is the berry crop of ground-dwelling herbs and dwarf shrubs (Dyke 1971; West 1982; Krebs et al. 2010).

The second approach of correlating abundance changes in voles with that in their food has been carried out in both *M. rutilus* (Krebs et al. 2010) and *M. gapperi* (Elias et al. 2006). In *M. rutilus*, Boonstra et al. (2001) proposed that abundant late summer–Fall berry crops permitted both good overwinter survival and good summer reproduction in voles the next year (see also Dyke 1971; West 1982). This hypothesis was supported by the findings of Krebs et al.

Table 2 Measures of variability of population density in *Myodes* populations from North America and representative studies in Eurasia

Continent	Species	Location	Latitude	<i>s</i> index		Coefficient of variation	
				Spring density	Fall density	Spring density	Fall density
North America	<i>M. rutilus</i>	Alaska ^a	64°51'	0.04	0.22	0.10	0.49
		Alaska ^b	64°51'	0.16	0.15	0.37	0.39
		NWT ^c	60°59'	0.39	0.42	0.89	1.00
		Yukon ^d	60°57'	0.39	0.40	1.83	0.57
	<i>M. gapperi</i>	NWT ^e	60°59'	0.30	0.42	0.86	0.93
		Manitoba ^f	50°11'	–	0.24	–	0.50
		Ontario ^g	48°30'	0.42	0.44	1.22	0.65
		Minnesota ^h	47°50'	–	0.44	–	0.63
		Maine ⁱ	43°45'	0.29	–	0.64	–
		Pennsylvania ^j	40°10'	0.38	0.28	0.75	0.52
Eurasia	<i>M. rutilus</i>	Oregon ^k	44°12'	0.43	0.32	0.72	0.82
		Kola Peninsula ^l	67°45'	–	0.29	–	1.47
	<i>M. glareolus</i>	South Siberia ^m	54°12'	0.29	0.16	0.58	0.36
		Pallasjärvi, Finland ⁿ	68°03'	0.67	0.85	0.74	0.78
		Kola Peninsula ^l	67°45'	–	0.65	–	1.21
		Poland ^o	52°45'	0.52	0.43	1.17	0.63
		England ^p	51°42'	0.42	0.32	0.83	0.51
		Czech Republic ^q	48°52'	0.76	0.74	1.46	0.97

The *s* index is included here mainly for historical reasons and the coefficient of variation is a better measure of population variability (McArdle and Gaston (1992))

^a West (1982), ^b Whitney and Feist (1984), ^c Fuller (1985a), snap-trapped data from his Table 1), ^d Boonstra and Krebs (2006), ^e Fuller (1977), snap-trapped data from his Fig. 2, ^f Mihok et al. (1985a), ^g Falls and Falls, unpublished data, ^h Krefting and Ahlgren (1974), ⁱ Elias et al. (2006) and Elias, Witham, and Hunter, unpublished data, ^j Merritt et al. (2001) and Merritt, unpublished data, ^k Gashwiler (1970), ^l Koshkina (1966), ^m Koshkina and Korotkov (1975), ⁿ Henttonen et al. (1987) and unpublished data, ^o Pucek et al. (1993), ^p Southern and Lowe (1982), ^q Tkadlec and Zejda (1998a)

Table 3 Autocorrelations of *Myodes* time series from North America for Fall estimates up to lags of 5 years

Population	Lag 1	SE (1)	Lag 2	SE (2)	Lag 3	SE (3)	Lag 4	SE (4)	Lag 5	SE (5)
<i>Myodes rutilus</i>										
Yukon, Canada ^a	–0.02	0.15	–0.52	0.15	0.12	0.19	0.21	0.21	–0.23	0.23
<i>Myodes gapperi</i>										
NWT, Canada ^b	0.07	0.27	0.13	0.27	–0.16	0.27	–0.13	0.28	–0.30	0.28
Manitoba, Canada ^c	0.25	0.25	–0.15	0.26	–0.11	0.27	0.17	0.27	0.09	0.28
Algonquin, Ontario ^d	0.39	0.17	0.15	0.19	0.03	0.19	–0.04	0.19	–0.14	0.19
Minnesota USA ^e	0.04	0.28	–0.37	0.28	–0.35	0.31	0.30	0.34	–0.01	0.36
Maine, USA ^f	0.05	0.20	–0.50	0.19	–0.24	0.19	0.25	0.18	0.05	0.18
Pennsylvania, USA ^g	0.12	0.22	–0.22	0.22	0.07	0.23	–0.14	0.23	–0.30	0.24

Statistically significant autocorrelations are shown in bold type

^a Boonstra and Krebs (2006), ^b Fuller (1977), snap-trapped data from his Fig. 2, ^c Mihok et al. (1985a), ^d Falls and Falls, unpublished data, ^e Krefting and Ahlgren (1974), ^f Elias et al. (2006), and Elias, Witham, and Hunter, unpublished data, ^g Merritt et al. (2001) and Merritt, unpublished data

(2010) in the Yukon. In turn, the abundance of the berry crop is driven by weather (combinations of monthly summer temperature and rainfall) 1 and 2 years earlier (Krebs et al. 2009). Thus, in *M. rutilus*, changes in abundance are set in motion 2–3 years earlier, acting first through weather that then impacts the flowering and ultimately the fruiting

of the dwarf shrubs. However, this cannot be the whole story. There is no indication of periodicity in the berry crops (Krebs et al. 2009), yet the Yukon vole populations are cyclic (Fig. 2; Table 3). Part of the problem may be that the berry crop series was too short—the changes in the berry crops was based on only 12 years of intensive work

Table 4 Autoregressive model estimates for *Myodes* populations from North America, following Bjørnstad et al. (1995)

Population	No. years	a_1	SE (a_1)	P (a_1)	a_2	SE (a_2)	P (a_2)	R^2
<i>Myodes rutilus</i>								
Yukon, Canada ^a	36	-1.01	0.11	0.001	-0.40	0.11	0.001	0.76
<i>Myodes gapperi</i>								
NWT, Canada ^b	12	-0.62	0.34	0.10	-0.18	0.38	0.64	0.30
Manitoba, Canada ^c	14	-0.72	0.27	0.02	-0.32	0.28	0.27	0.49
Algonquin Park, Ontario ^d	34	-0.42	0.18	0.03	-0.03	0.18	0.87	0.22
Minnesota, USA ^e	11	-0.93	0.34	0.03	-0.50	0.64	0.45	0.50
Maine, USA ^f	21	-1.02	0.21	0.001	-0.92	0.42	0.04	0.58
Pennsylvania, USA ^g	13	-0.69	0.25	0.01	-0.07	0.25	0.77	0.36

Fall population estimates were used unless otherwise noted. Statistically significant parameters are in bold type

a_1 is a measure of direct density dependence, and a_2 a measure of delayed density dependence

^a Boonstra and Krebs (2006), ^b Fuller (1977), snap-trapped data from his Fig. 2, ^c Mihok et al. (1985a), ^d Falls and Falls, unpublished data, ^e Krefting and Ahlgren (1974), ^f Elias et al. (2006) and Elias, Witham, and Hunter, unpublished data, ^g Merritt et al. (2001) and Merritt, unpublished data

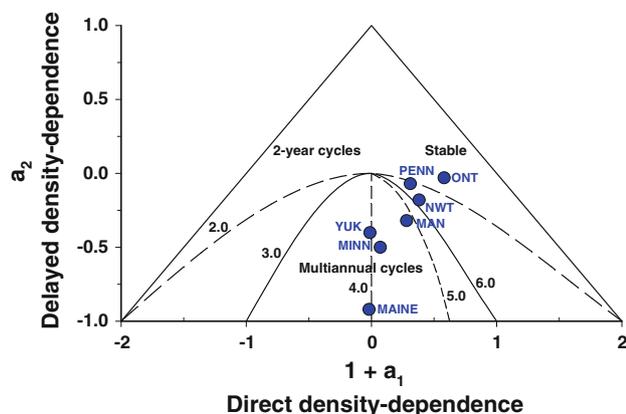


Fig. 6 Coefficients of the second-order autoregressive model for North American *Myodes* data. Below the semi-circle, the dynamics are predicted by this model to be cyclic, and the cyclic period increases from left to right. Two contours of cycle length (3.5 and 4.5 years) are indicated. MINN Minnesota, MAN Manitoba, NWT Northwest Territories, PENN Pennsylvania, and ONT Ontario data for *M. gapperi*. YUK Yukon data for *M. rutilus*

versus that on the voles of 33 years. In addition, there is no evidence for cyclicity in weather patterns on the scale of the 3- to 5-cycle in *M. rutilus*. One possible explanation is that there is memory in the dwarf shrubs, as there is in oaks (Sork et al. 1993), such that it takes time for the plants to build up resources to produce bumper crops of berries. Thus, they cannot have successive bumper crops even if weather conditions are suitable.

In cyclic *M. gapperi* from Maine the critical food appears to seed production from masting white pine (*Pinus strobus*) (Elias et al. 2006), with peaks in masting preceding 4 of 5 peaks in voles. Thus, it is not unequivocally clear that pine mast is driving the cycles in these voles. Of the masting species in these forests, four other tree species

produce more mast than the white pine (red oak, *Quercus rubra*: 26 times more), but the vole dynamics are not correlated with these nor do the voles eat the acorns (of the oaks) or other tree seeds (*Picea rubens* or *Acer rubrum*) readily. If white pine seeds are critical most of the time, weather presumably determines when the mast will occur (Matthews 1963; Ostfeld and Keesing 2000). The same problem occurs as with *M. rutilus*, how to get cyclicity in mast when weather does not show that periodicity, and so too a possible solution, as pines need time to recover from a masting event and build up their resources.

Nutrients

The bottom-up control of vole populations through nutrients is one possible explanation for population fluctuations. Boonstra et al. (2001) and Boonstra and Krebs (2006) hypothesized that snowshoe hares (*Lepus americanus*), because of their extensive herbivory at the peak of their 10-year cycle, indirectly caused population peaks in red-backed voles 2–3 years later. This could occur because the berry-producing dwarf shrubs were stimulated by the flush of nutrients released by the decomposition of large quantities of fecal pellets produced by hares at their population peak. Though the nutrients are released primarily in the summer following their accumulation in feces in winter, lags are introduced into this system because it takes 2 years to produce a good berry crop (the plants take up the nutrients the first summer producing a bumper crop of berries the next) and a third to get peak populations of voles. We now tentatively reject this hypothesis, as Cowcill (2006), by adding nutrients at the expected level from decaying hare fecal pellets, was neither able to influence berry production nor vole demography.

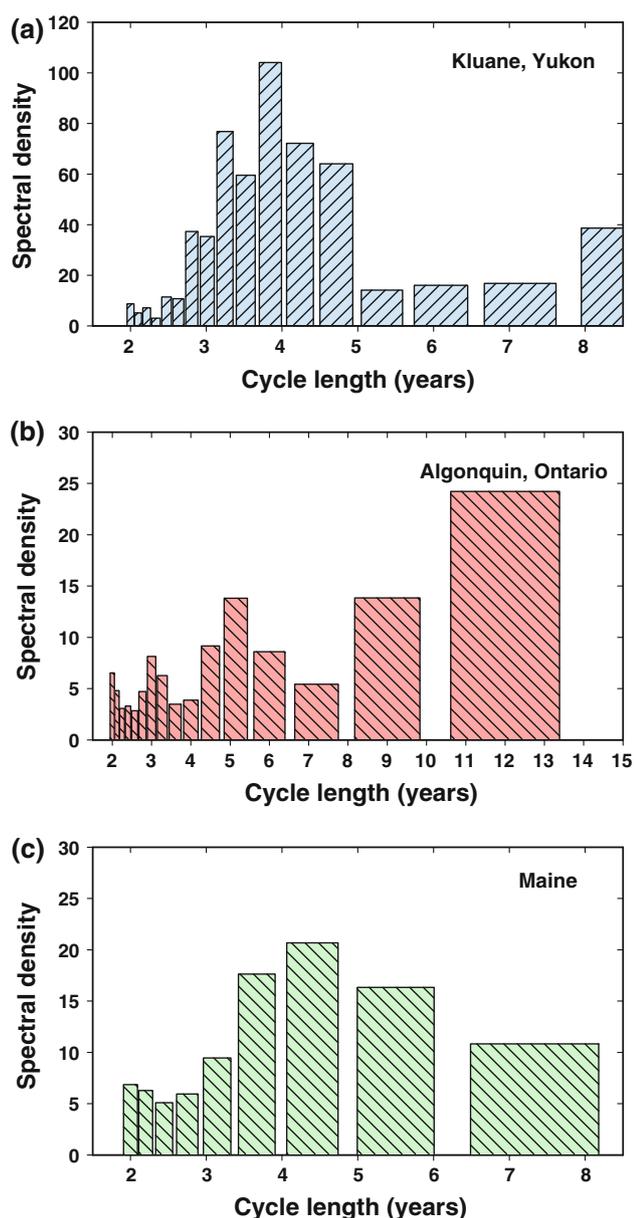


Fig. 7 Spectral densities of *Myodes* populations. Spectral densities were smoothed by a weighted moving average. **a** The Kluane, Yukon population of *M. rutilus* shows a clear spectral peak in the 3- to 5-year range. **b** The Algonquin *M. gapperi* shows no clear spectral peak until one reaches 11–13 years, well beyond the range of 3- to 4-year cycles. **c** The Maine data for *M. gapperi* shows a spectral peak in the 3- to 5-year range, not unlike that of Kluane (**a**)

Predation

Predation may play an essential role in the population dynamics of northern small mammal populations. In Fennoscandia, microtine populations (*Microtus* spp.) in the south do not cycle because of strong functional responses by a large suite of generalist predators that may limit their numbers (Erlinge et al. 1983, 1984). In contrast, those in

the north (both *Microtus* spp. and *Myodes* spp.) do or have until recently shown cycles (Korpimäki and Norrdahl 1991; Klemola et al. 2002; Hörnfeldt et al. 2005), and these are caused by delayed numerical responses of specialist predators, primarily least weasels (Henttonen et al. 1987; Korpimäki et al. 1991; Oksanen et al. 2000). However, cycles of *Myodes* spp. appear to be a by-product of those in *Microtus* spp. with the former in the forests acting as alternative prey once the latter in the adjacent grasslands have declined (Henttonen et al. 1987; Korpimäki et al. 2005). Given that most North America *Myodes* populations do not cycle, either generalist predators play a pre-eminent role in limiting vole numbers (as in southern Fennoscandia), specialist predators act differently in North America, or predators are largely irrelevant determinants of vole population processes. The evidence from North America suggests the last explanation is correct.

Many species of avian and mammalian predators in North America prey on *Myodes* spp. (Alexander and Verts 1992; Doyle and Smith 2001; Martin 1994; Merritt 1981; O'Donoghue et al. 2001; Rohner et al. 2001; Prugh 2005), but none specialize on them. The main generalist mammalian predator in the boreal forest—the coyote (*Canis latrans*)—has little or no impact on *M. rutilus* (O'Donoghue et al. 1998; Prugh 2005), eating primarily snowshoe hares when these are abundant, and in the Yukon eating *Microtus* voles, but not *M. rutilus*, when hares are rare (O'Donoghue et al. 1998). In Alaska, Prugh (2005) found no prey switching by coyotes to voles when hares were scarce. Similar results were found for *M. gapperi* in Alberta, with 89% of the voles eaten being *M. pennsylvanicus* and, in winter, both vole species contribute <12% of winter diet (in summer and Fall they contribute 10–34%) (Todd et al. 1981). The main generalist avian predator in the boreal forest—the great horned owl (*Bubo virginianus*)—takes *M. rutilus* voles in proportion to their abundance, but does not actively select for them nor switch to them (Rohner et al. 2001). In the aspen parkland, *M. gapperi* is markedly under-represented in this owl's diet relative to its abundance (Rusch et al. 1972). Only one experiment has assessed the impact of predators, excluding only larger mammalian predators of *M. rutilus*, but not the smaller ones (i.e. the mustelids), and it failed to alter vole demography (Boonstra and Krebs 2006). Thus, the generalist predators appear to have little influence on *Myodes* dynamics and in general these voles contribute little to their diet.

The assessments on the impact of specialist mustelid predators have been either anecdotal (e.g., Miller and Getz 1977), correlational (Johnson et al. 2000), or based on lack-of-capture/lack-of-sighting evidence. Over vast stretches of the boreal forest, specialist mustelid predators are rare. In Alaska, neither Whitney (1976) nor West (1982) make any

mention of predators. In the Yukon, Boonstra et al. (2001) report that during an intensive 10-year study only 9 *Mus-tela erminea* were captured at Kluane Lake, and this rarity was reinforced by all the work from 1973 to 2009 in the area (e.g., Gilbert and Krebs 1981; Krebs et al. 2009). O'Donoghue et al. (2001b) report that over 10 years in the same area, only 3 marten (*Martes americana*) were seen and tracks were infrequent. In the SW Yukon, Slough (1989) reported marten to be uncommon over large areas. In the NWT, neither Fuller (1969, 1977, 1985a, b), from over 15 years of snap-trapping and live-trapping small mammals at Heart Lake, nor Martell and Fuller (1979), from 3 years trapping in the tundra-taiga subarctic area near Inuvik, make any mention of capturing mustelids. Fuller (1977) reported that neither indices of marten nor of weasels changed with vole density.

The densities of *M. rutilus* in North America are so low in all populations most of the time (Table 1) that the likely candidates for specializing on them—the weasels (*M. erminea* and *M. nivalis*) and marten—are constrained by food shortage, particularly overwinter and in Spring. Erlinge (1974) in southern Sweden and Tapper (1979) in England found that *M. nivalis* required minimum Spring densities of 10/ha and 14/ha field voles (*M. agrestis*), respectively, before they would breed. The average Spring densities never reached those values (Table 1 we discount the estimates of Whitney and Feist 1984 as overestimates because of small trapping grid size), though in the occasional Spring, densities approach or exceed them (Gilbert and Krebs 1981; Schweiger and Boutin 1995; Boonstra and Krebs 2006). Thus, with low densities prevailing over large areas for extended periods of time, the specialist mustelids must have a high probability of going extinct locally (Jędrzejewski et al. 1995). Occasionally, when *Microtus* spp. populations increase in the meadows for a sustained period, weasel populations may increase and then impact the *M. rutilus* populations in the adjacent forested areas (Boonstra et al. 2001). This may explain the findings of Johnson et al. (2000). They analyzed *M. erminea* records from fur-trading posts from northern Manitoba and Ontario (1915–1940) and found evidence of cycling in 20 of 45 of them, with two being continuously cyclic. They speculated that these cycles were a reflection of population changes in the small mammals, possibly in *M. gapperi*. Unfortunately, we have no small mammal density data for any of these central boreal forest sites to see how they compare with those of the northwestern boreal forest. Given the evidence from Fennoscandia and the Yukon, these weasel cycles are more likely to be a reflection of changes in *Microtus* populations. In the mixed deciduous-coniferous forests of central Ontario, Fryxell et al. (1998) found no cycles in *M. gapperi*, but did find a significant correlation between the population growth rates of *M. gapperi* and six other

small mammal species. They argued that this relationship could not be a result of these species tracking variation in a common food item as they ate different foods. They suggest that the likely synchronizing factor was predation, most likely marten. In central Alberta, Keith and Cary (1991) found that the main factor explaining the changes in four mustelid species was changes in the density of snowshoe hare with the 10-year cycle, but that changes in densities of *M. gapperi*, *M. pennsylvanicus*, and *P. maniculatus* improved the predictive relationship only slightly. We conclude that predation whether by generalist or by specialist mammalian predators does not explain the lack of cycles in northern *Myodes* populations, but further research is required in southern populations.

Two small specialist avian predators—the boreal (or Tengmalm's) owl (*Aegolius funereus*) and the northern hawk owl (*Surnia ulula*)—clearly do not prevent red-backed vole population cycles, but changes in their numbers may be indicative that cycles are occurring. In Fennoscandia, the boreal owl is a nomadic vole specialist that responds to low prey density in the north by moving south (Korpimäki 1986; Sonerud et al. 1988). In eastern North America, Cheveau et al. (2004) provide suggestive evidence that the boreal owl shows 4-year irruptions into southern regions of North America, and they argue this may be indicative of 4-year cycles in *M. gapperi*. The hawk owl and the great gray owl (*Strix nebulosa*) show range extensions at the same time. However, it is much more likely that the movements of these three owl species were indicative of fluctuations in *Microtus* voles, not *M. gapperi*, as the former constitute the major small mammal prey in the boreal forest in spite of the fact that the latter are the most abundant small mammal in these forests (boreal owls, Doyle and Smith 2001; northern hawk owls, Rohner et al. 1995; great gray owls, Nero 1980). Even in Fennoscandia, the primary prey of the boreal owl are *Microtus* voles (Korpimäki and Norrdahl 1989). Thus, changes in density patterns of these specialist owls are not indicative of changes in *Myodes* populations.

Disease and parasites

The impact of disease and parasites on the demography of North American red-backed voles is unknown. As with their counterparts in Eurasia, they are infected by a host of bacteria, viruses, and internal and external parasites (Merritt 1981; Alexander and Verts 1992). In the UK, disease may help to produce the delayed density dependence in *M. agrestis*, playing a causal role in their cycles (Burthe et al. 2008; Smith et al. 2008). In Fennoscandia, hantavirus reduces overwinter survival in *M. glareolus* (Kallio et al. 2007). However, because of its vole-to-vole transmission pattern, it rapidly disappears at low density. In

North America, hantavirus infects *Peromyscus*, not *Myodes* spp. Thus, because low density and non-cyclicity characterizes the populations *Myodes* spp. over much of their range in North America, diseases with similar transmission requirements and survival impacts are unlikely to play a significant role in their demography. For infections with less pronounced survival impacts, long-term survival in *Myodes* may be independent of vole density (Haukisalmi et al. 1988). However, the interactions between sublethal infectious diseases and other factors (e.g., low resource availability, bouts of severe weather, etc.) may be relevant in *Myodes* (see Pedersen and Greives 2008 for factorial experiment in *Peromyscus*). We tentatively conclude that the disease–parasite hypothesis does not explain *Myodes* demography, but recognize that no experimental work has been done on this hypothesis.

Interspecific competition

If other species compete with *Myodes* species for space or food, this could operate to keep populations perpetually low. *Peromyscus* spp. are the main woodland rodents that live side by side the *Myodes* spp. throughout North America that could potentially affect the demography of the latter. They do not as neither Galindo and Krebs (1985) nor Gilbert and Krebs (1981) found any relationship between the numbers of *P. maniculatus* and those of *M. rutilus*. Similarly, neither Miller and Getz (1977) with *P. leucopus* in Connecticut, Morris (1983) with *P. maniculatus* in Alberta, Mihok et al. (1985b) with *P. maniculatus* in Manitoba, nor Bowman et al. (2008) with *P. maniculatus* in Ontario found any relationship between their numbers and those of *M. gapperi*. The dominant intermediate-sized herbivore across the boreal forest is the snowshoe hare and again there is no evidence for competition between it and *Myodes* (Boonstra and Krebs 2006).

Similarly, there is little evidence that significant competition occurs between *M. rutilus* and *Microtus* voles in the northern boreal forests. *Microtus* voles (either *M. pennsylvanicus* and *M. oeconomus* or both simultaneously) occupy primarily grassy regions within the northern boreal forest (meadows, marshes, and forest) or grasslands beside the forest, and may either enter the adjacent forests occasionally or prevent *M. rutilus* from entering the grasslands. In the Yukon, we occasionally captured *Microtus* voles on the forest grids but they were rare (<4 voles/grid/year on 13 2.81-ha grids trapped for 8 years) (Boonstra et al. 2001). However, we found no relationship between the population sizes of the *Microtus* voles and those of *M. rutilus* and nor were the population dynamics of *Microtus* in grassland related to those of *M. rutilus* in the forest (i.e. population growth in one species was not associated with a decline in the other). In their

intensive studies on *M. rutilus* in the boreal forests of Alaska, both Whitney (1976) and West (1982) simultaneously captured *M. oeconomus*, but the population dynamics of one species was unrelated to that of the other. In his 11-year study of small mammals in the boreal forests of the NWT (both *Myodes* species studied), Fuller (1985a, b) makes no mention of *Microtus* voles. Other *Microtus* species may overlap the distribution of *Myodes* species (e.g., *M. xanthognatus*, Conroy and Cook 1999; *M. miurus*, Galindo and Krebs 1985), but either because of more localized distributions, more specialized habitat requirements most of the time, or low densities most of the time, these are unlikely to explain lack of cycles in *M. rutilus*. We conclude that the population dynamics of *M. rutilus* is not affected by interspecific competition with *Microtus* voles.

In contrast, competition between *M. gapperi* and *M. pennsylvanicus* in the southern forests may occasionally occur. Observational evidence from islands indicates that *Microtus* will inhabit forests if *Myodes* are absent (Cameron 1964). Observational evidence that one species will enter the primary habitat of the other and become resident (i.e. *M. gapperi* will enter grasslands and *M. pennsylvanicus* will enter woodland) only in winter when both are not breeding and agonistic behavior is minimal (Iverson and Turner 1972; Morris 1969; Turner et al. 1975). In contrast, during the breeding season, tight habitat separation is maintained (Morris 1969), apparently with *M. gapperi* being able to exclude *M. pennsylvanicus*. Experimental evidence suggests that interspecific competition does occur, separating the two species into their favored habitat types (Grant 1969; Morris and Grant 1972; but see criticisms of methods and interpretation by Galindo and Krebs 1986). However, these findings do not explain the failure of cycles in *M. gapperi* over the majority of the dominant forest habitats it occupies where *Microtus* plays little or no role.

Weather

Severe winter weather may account for the lack of cycles in North America whereas milder but more predictable winters may account for their presence in Fennoscandia (Hansen et al. 1999). This could operate either directly (by reducing survival at key times overwinter), indirectly (by reducing plant productivity), or sequentially (low plant productivity creating marginal food conditions and thus affecting overwinter survival). Relative to northwestern Eurasia where the most intense research on cycles has taken place (Fennoscandia, Great Britain, and central Europe), major continental effects produce a climate over northern and central North America that is 10–20°C lower in January (Seager 2006). In the summer growing season, this translates into reduced primary productivity,

which is much less in the North American boreal forest than in Fennoscandia (Bonan and Shugart 1989). Huston and Wolverton (2009) in their analysis of net primary production in forests present data suggesting that annual leaf litter biomass production is 78% higher in Fennoscandian forests than in North American forests north of latitude 60°N.

Regular exposure to severe environmental conditions at the onset or end of winter could potentially cause declines in *Myodes* populations. Formozov (1946) and Pruitt (1957) postulated that there is a critical period in the Fall when ambient temperatures may drop below ground temperatures, leaving small mammals thermally stressed. It is only when snow depth reaches 15–20 cm that small mammals are buffered from extreme temperatures fluctuations. Snowmelt in the Spring is another critical period when delayed snowmelt and accumulation of melt water floods nest sites and tunnels in the subnivean space. Though these periods of environmental stress may occasionally occur and cause poor survival (see references in Merritt and Merritt 1978; Mihok and Schwartz 1989), they are infrequent and cannot explain the lack of cyclicity. In Alaska, Whitney (1976) found periods of good winter survival despite extremely low ground temperatures. After 12 years of work in the NWT, Fuller (1977) rejected the critical period hypothesis, concluding that a population's ability to withstand the stresses of winter varied over time and that some unknown property (possibly related to food) was responsible for better survival in years when winter conditions were more severe. This conclusion was echoed by Mihok and Schwartz (1989), who experimentally examined the key physiological change—*anemia*—resulting from exposure to low temperature. They were unable to find a clear relationship between winter survival and winter weather in southern Manitoba, with periods of good survival often being associated with low temperatures. The only clear result was that short-term exposure to extreme temperatures (−20 to −30°C) resulted in *anemia* caused by blood loss through the stomach epithelium. However, not all animals were equally susceptible to temperature-induced *anemia*, with unknown factors (e.g., possibly stress, disease, condition) also playing a role with the resulting variability in expression of *anemia* in wild populations. In *M. rutilus* from Alaska, Sealander (1966) also reported that 11–15% were *anemic* in the period between December and March. In summary, winter weather patterns experienced over the broad distributional range of *Myodes* in North America cannot explain the lack of cyclicity.

Climate change may be bringing back the winter weather hypothesis, but under a different guise. Fennoscandia has been experiencing a deterioration in the predictability of winter weather, operating through more

frequent thaws, shorter periods of protective snow cover, and ice formation at ground level. This unpredictability may be associated with reduced overwinter survival and an attenuation of cycles (Henttonen and Wallgren 2001; Hörnfeldt et al. 2005; Ims et al. 2008). A truncation of a peak vole population occurred in southern Ontario that was caused by winter rains followed by intense cold (Boonstra and Rodd 1983). In the southern Yukon, similar mid-winter thaws and occasional rains are now occurring, and these may be responsible for the local extinction of arctic ground squirrel populations (Donker and Krebs, personal communication).

Spacing behavior and social control

Myodes in North America have the behavioral organization in which spacing behavior can potentially limit breeding density. In cyclic microtine populations, age structure shifts significantly to older animals as the cycle progresses (Boonstra 1994; Tkadlec and Zejda 1998a), and this is fundamentally tied to density-dependent inhibition of maturation in juveniles (reviewed in Oli and Dobson 1999, 2001). If this inhibition does not occur, population cycles are absent (Boonstra 1994; Tkadlec and Zejda 1998b; Oli and Dobson 2001). Both the lack of inhibition and the lack of cycles occur most of the time in North American *Myodes* populations.

Initially, adult males were thought to be the cause of this inhibition and of the poorer survival at higher density. However, in *Myodes* spp., breeding males have extensively overlapping home ranges, whereas breeding females are territorial, having mutually exclusive home ranges in both *M. gapperi* (Mihok 1979; Perrin 1979b; Bondrup-Nielsen 1987) and *M. rutilus* (Burns 1981; Gilbert et al. 1986). Removal of adult breeding males has been carried out three times in *M. gapperi* with no clear impact on juvenile survival or maturation (Bondrup-Nielsen 1986; Elliott 1969; Watts 1970). In contrast, removal of adult breeding females resulted in juvenile females maturing at younger ages in both *M. gapperi* (Bondrup-Nielsen 1986) and *M. rutilus* (Gilbert et al. 1986), but no improvement in either male or female juvenile survival in the latter study (it was not assessed in *M. gapperi*). Thus, the pattern of female territoriality and social control of reproductive rates are similar to those found in Eurasian species (Bujalska 1973; Saitoh 1981; Tkadlec and Zejda 1998a) resulting in an inhibition of maturation at peak densities (Kalela 1957; Koshkina and Korotkov 1975; Prévot-Julliard et al. 1999). This density-dependent social inhibition seldom occurs in North American populations because population density early in the breeding season is usually too low (Miller and Getz 1977; Fuller 1979; Mihok 1979; Burns 1981; West 1982; Gilbert and Krebs 1981).

Interactive effects

The above discussion approaches the problem of population limitation and cyclicity in red-backed voles through the lens of a single factor view of the world. This is the most parsimonious, initial approach in trying to tease out cause (one of these factors) from their effect (the repeated pattern of demographic changes) and is one laid out by Chitty (1967). Is the cause both necessary and sufficient to produce the effect? There may be factors (e.g., severe winter weather) which may be sufficient to cause the decline in vole numbers in winter, but not necessary (e.g., though some declines are correlated with severe weather, in other winters voles may decline in spite of good weather). Ostfeld (2008) has argued that this single factor approach is too simplistic and that interactions between two or more of the above factors could explain demographic patterns, as they may in *Peromyscus* (Pedersen and Greives 2008). These types of interactive effects explain most of snowshoe hare cyclic demography (predation predominantly, but interacting with food, to cause declines, Krebs 1995; with effects of predation acting to maintain low numbers for a period of time thereafter, Sheriff et al. 2010, 2011). However, we think that this explanation is likely only when the key factor is present (such as sufficient food), but the population declines anyway or does not increase as expected (because of the actions of other factors, such as parasitism or predation). These interactive effects are unlikely to explain red-backed vole populations at persistently low densities, but may explain some of their declines from high density. The key take-home message is that only by appealing to factorial experiments, if warranted by the demographic pattern, will the role of single factor versus interactive factors be resolved.

Conclusions

Our statistical analysis of all long-term studies and our review of all the published literature on *Myodes* spp. in North America lead us to reject tentatively seven of eight potential explanations for the lack of cycles in these species, though they may to varying degrees play a role in their demography. Three are rejected because experimental evidence wholly or largely is against them (spacing behavior and social control, interspecific competition, and nutrients) and four because the weight of evidence provides little or no support for them (predation, disease and parasites, weather, and interactive effects). Our understanding of the latter (particularly predation and disease and parasites) could be strengthened by experimentation. The major difference between *Myodes* population dynamics in Europe and North America in the role of predation could be tested

directly by large scale predator manipulation experiments like those done by Korpimäki et al. (2005).

There are two important messages that follow from this review. First, North America is short of rigorous long-term studies of population changes in *Myodes* species. The contrast here with the extensive Fennoscandian time series data on *Myodes* species is particularly strong. Long-term data series should be gathered within an experimental framework. The second message from our review is that experimental manipulations of food supplies over several years would be a valuable addition that would test our conclusions about food limitation in *Myodes* population dynamics in North America.

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