Journal of Mammalogy, 96(3):573–578, 2015
DOI:10.1093/jmammal/gyv062

Cyclic dynamics of a boreal southern red-backed vole population in northwestern Quebec

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In Fennoscandia, red-backed vole populations (*Myodes* spp.) often show regular fluctuations of abundance of 3- to 5-year periods. In contrast, only a few populations show evidence of cyclic fluctuations in North America. From 2001 to 2009, we livetrapped southern red-backed voles (*Myodes gapperi*) in 3 mature jack pine and 3 mature black spruce forest stands in the Muskuchii hills region, Quebec, Canada. We found that their density fluctuated (up to 41-fold) with a cyclical pattern and 4-year periods. Our study is the first to demonstrate cyclic dynamics in a southern red-backed vole population found in the boreal forest of North America. Regular pulse of food or heavy predation may be responsible for the fluctuations of southern red-backed voles. Furthermore, vole cycles may help elucidate the factors driving the irruptions of owls in the boreal forest.

Key words: *Clethrionomys*, population dynamics, population regulation, rodents, small mammals

Populations of small rodents showing regular fluctuations of abundance have fascinated both the layman and the scientific community for almost 100 years (Elton 1924; Krebs 2013). Cyclic populations of voles typically are fluctuating with a period of 3–5 years (e.g., *Myodes rutilus*—Korpimäki et al. 2005; *Myodes rufocanus*—Stenseth 1999). Several hypotheses were developed to explain cycles such as intrinsic regulation (Chitty 1960), bottom-up (Turchin et al. 2000; Elias et al. 2006) and top-down regulations (Korpimäki and Krebs 1996), and climate change (Kausrud et al. 2008). The general lack of consensus on what are the main factors driving cycles may be due to biotic and abiotic factors that are intrinsic to the different geographical locations of rodent populations (Korpimäki and Krebs 1996; Oksanen and Oksanen 2000; Pitelka and Batzli 2007).

In Fennoscandia, there is substantial literature documenting cyclic dynamics in several red-backed vole populations (*Myodes* spp.), especially in boreal forests (Stenseth 1999). In North America, red-backed voles typically fluctuate in abundance, but only a few populations are cyclic (Elias et al. 2006; Boonstra and Krebs 2012). However, few studies have examined the long-term fluctuations of abundance of red-backed voles in the northern boreal forests of Canada. Indeed, most populations documented by Boonstra and Krebs (2012) were in the hemiboreal forest, where the primary productivity and tree species diversity are higher compared to the northern boreal forest (Brandt 2009). Primary productivity is an important factor involved in population dynamics (Oksanen and Oksanen 2000) and may be responsible for causing certain populations to fluctuate cyclically based on a recurrent biotic event (e.g., high predation years, mast years).

Predation has often been involved in explaining small rodent cycles because of its delayed-density-dependent effect on the prey population growth. As a result, predators respond numerically to their prey abundance but with a delay of 1 or 2 years (Hanski et al. 1993). In both northern boreal forests of Fennoscandia and the tundra of the high Arctic, predators showed numerical and functional responses to fluctuating abundances of voles and lemmings and studies have shown that they may be responsible for the cyclic dynamics of the small rodents (Korpimäki and Krebs 1996; Gilg et al. 2006; Therrien et al. 2014). In the boreal forests of eastern Canada, several birds of prey and small predatory mammals (e.g., mustelids) are characterized by similar numerical fluctuations. However, the relationship between their fluctuations and the abundance of their prey is still unclear. Cheveau et al. (2004) suggested that the regular 4-year irruptions of 3 species of owls in the boreal forest were a direct response to cyclic population dynamics of small mammals. Johnson et al. (2000) also showed that ermine (*Mustela erminea*) often fluctuated regularly along a latitudinal gradient and they suggested that it was in accordance with the abundance of southern red-backed voles (*Myodes gapperi*), the most common cricetid species in the forests of eastern Canada. Although several species of owl and the ermine appear to fluctuate regularly in response to their prey abundance, there is still no clear evidence that populations of southern red-backed voles fluctuate cyclically in the boreal forests of eastern Canada.

In this study, southern red-backed voles were trapped for a period of 9 years (2001–2009) covering 2 complete fluctuations of abundance in the Muskuchii hills, western Quebec, Canada. Based on the regular owl irruptions documented by Cheveau et al. (2004) in our study area, we hypothesized that the Muskuchii hills population was cyclic. We predicted 1) autocorrelation in the time series because cyclic populations of small rodents typically fluctuate according to 3- to 5-year periods. We further predicted that 2) the population would show delayed density dependence in the autoregressive model, a necessary condition for cycles (Turchin and Hanski 2001).

Materials and Methods

Study area.—Our study area was located in the boreal forest of western Quebec, Canada, in the region of the Muskuchii hills (50°12′N, 78°44′W). It was located in the black spruce-feather moss bioclimatic domain (Gauthier et al. 2000). Two types of mature forests were found in our study area: black spruce forests and jack pine forests, depending on the soil water regimes. The first type of forest was mainly composed of black spruce (*Picea mariana*) with sheep laurel (*Kalmia angustifolia*), blueberries (*Vaccinium* spp.), and feather mosses (e.g., *Pleurozium schreberi*, *Dicranum polysetum*) as understory vegetation (Bescond et al. 2011). The latter type of forest was mainly composed of jack pine (*Pinus banksiana*) with terrestrial lichens (*Cladina* spp.) as understory vegetation (Boudreault et al. 2002). Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*) may be occasionally found in both forests.

Small mammal sampling.—Small mammals were live-trapped in 6 sites: 3 mature black spruce-feather moss stands and 3 mature jack pine stands. From 2001 to 2009 inclusively, we used one 120 × 120 m trapping grid (49 stations) per site in which we activated one Sherman SFG trap (H.B. Sherman Traps, Tallahassee, Florida) per station. From 2003 to 2009, we added 13 pitfall traps in each grid (at 1 station of 4) in order to include adequate sampling for shrews. Moreover, we further added one large Sherman LFG trap in each corner of the trapping grids and another one in the center from 2004 to 2009. Although pitfall traps and large Sherman traps were used to capture shrews and weasels, respectively, both traps were also used to capture voles and mice. Each station was separated by 20 m and the area covered by each trapping grid was 1.44 ha. Each Sherman SFG trap was baited with peanut butter and a piece of apple, and cotton batting was placed in the traps for warmth. Large Sherman LFG traps were baited with sardines. However, they were added to the total trapping effort because rodents were frequently captured in them. Sprung traps were assigned the value of 0.5 when we calculated trapping effort.

Traps were activated for 3 consecutive nights. We trapped small mammals between 4 July and 24 July for all years, except in 2002 (18 June–24 June) and 2003 (31 July–6 August) because of logistical constraints. All captured small mammals were identified to species, weighted, sexed, and ear-tagged with a unique-number 1005-1 Monel tag (National Band & Tag Company, Newport, Kentucky) before release as recommended by the American Society of Mammalogists (Sikes et al. 2011). Identification of small mammals was done according to the key of Lupien (2002).

Statistical analyses.—All statistical analyses were run with the software R version 3.1 (R Development Core Team 2014). Because southern red-backed voles were livetrapped and marked, we used spatially explicit capture–recapture models (Efford and Fewster 2013) to estimate their yearly densities for each site. We used the package "secr" implemented in R (Efford 2014). Trapping grids varied according to the number of traps due to the addition of pitfall traps in 2003 and LFG Sherman traps in 2004. Thus, we estimated the densities according to 3 periods (3 different models): 2001–2002, 2003, and 2004–2009 trapping campaigns. Densities were averaged according to the type of forest stand and the respective variances were calculated with the delta method (Powell 2007). We used the minimum number alive of voles when less than 5 voles were captured or when the spatially explicit capture–recapture models could not converge (Krebs 1966). Densities were estimated with the maximum likelihood approach with a 100-m buffer (Krebs et al. 2011). Elias et al. (2006) argued that the catch per unit effort may provide different estimates than with capture–recapture methods. In the current study, both estimates were highly correlated for both types of forest stands (black spruce: Pearson's $r = 0.99$; jack pine: $r = 0.98$). Thus, we focused on the capture–recapture estimates as these estimates are closer to reality by considering imperfect detection (Efford and Fewster 2013).

To test statistically whether the population of Muskuchii hills showed cyclic dynamics or not, we estimated autocorrelation coefficients between the densities at time t (or year t) and times $t + 1$, $t + 2$, $t + 3$, $t + 4$, and $t + 5$ with simple linear models. A high negative correlation indicates the lag at which the amplitude is maximized, while a high positive correlation indicates the length of the period. Both are necessary to support regular fluctuations of densities. Density dependence of the population dynamics was determined with 2nd-order autoregressive models (Venables and Ripley 2002). After we log-transformed the densities, we fitted the following log-linear model: $X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2 X_{t-2} + \varepsilon$, where X_t is the log-transformed density of southern red-backed voles at time t, β_0 is the intercept, β_1 is the coefficient for direct density dependence, β_2 is the coefficient for delayed density dependence, and ε is the error term (Bjornstad et al. 1995; Stenseth 1999). The length of the periods may be determined by plotting the coefficients on the graphical representation of the model of Royama (1992). The R code and the data can be consulted in Supporting Information S1 and S2, respectively.

RESULTS

From 2001 to 2009, we captured 301 individual southern red-backed voles with a total effort of 9,679 trap-nights. The time series of the southern red-backed vole population showed 2 major fluctuations of densities in both types of forest stands (Fig. 1). However, the amplitude of the fluctuations was more pronounced in the black spruce forest sites (increase by 41-fold between 2005 and 2006). In 2001, no southern red-backed vole was captured. Voles reached high densities in 2002 and continued to increase until 2003. The population then declined to very low levels in 2004. In 2005, the decline continued to even lower levels. The population then increased to high levels for 2 consecutive years (2006–2007). In the black spruce forest stands, the population reached low densities in 2008 and continued to decline in 2009. In the jack pine forest stands, voles slightly declined in 2008 and reached very low densities in 2009. Detailed statistical results of the spatially explicit capture–recapture models can be found in Supporting Information S3.

For both forest stands, the autocorrelation analyses showed a high negative correlation between the abundance measured at time t and at time $t + 2$ ($r_{t,\,t+2}$; Table 1). A high positive correlation was observed between the abundance measured at time t and at time $t + 4$ ($r_{t,\,t+4}$). Direct density dependence and delayed density dependence were supported statistically for both black spruce and jack pine forest sites (Table 1). Both coefficients (β_1 and β_2) estimated with the 2nd-order autoregressive model were significant according to the 95% confidence interval that did not include 0. When plotted in the phase plane diagram presented by Bjornstad et al. (1995), the Muskuchii hills population corresponds to 4-year multiannual cycles, which supports the autocorrelation results (Fig. 2).

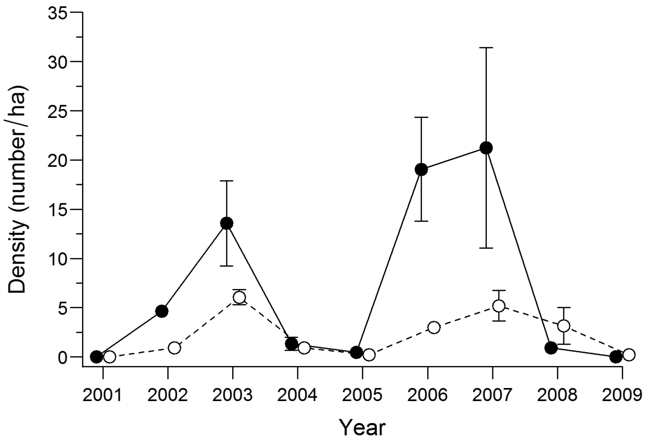

Fig. 1.—Time series of the southern red-backed vole (*Myodes gapperi*) population of the Muskuchii hills in black spruce (black circles; solid line) and jack pine (white circles; dotted line) forest sites. Densities and their respective standard errors are presented.

DISCUSSION

Our study is the first to find cyclic dynamics in a southern red-backed vole population in the boreal forest of Canada. With respect to our 1st hypothesis, the autocorrelation analysis shows that the population is affected by regular fluctuations of abundance with a period of 4 years. Large amplitude fluctuations characterized black spruce forest sites (up to 41-fold increase), while small amplitude fluctuations were observed in the jack pine forest sites (up to 7-fold increase). Furthermore, the autoregressive analysis indicates that voles show both direct and delayed density dependence in the 2 forest types, which are necessary for a population to be considered cyclic. The statistical support shown in the current study reinforces the hypothesis that cyclicity in red-backed vole populations of North America may be more frequent than previously suggested (Boonstra and Krebs 2006, 2012).

Previous studies have found that food may be responsible for the cyclic fluctuations of certain red-backed vole populations. Elias et al. (2006) have shown that the high abundance years of southern red-backed voles in Maine coincided with mast years of the white pine (*Pinus strobus*). Boonstra and Krebs (2012) suggested that the periodic fluctuations of food such as berries are responsible for generating cycles in the northern red-backed vole populations (*M. rutilus*). Southern red-backed voles were more abundant in the black spruce forest sites than in the jack pine forest sites, which supports previous studies showing high habitat use in mature black spruce forests (Fauteux et al. 2012). Black spruce is one of the most widespread species that dominates the northern boreal forests of eastern Canada and previous studies reported high production years every 4 years (Burns and Honkala 1990). In our study area, Messaoud et al. (2007) reported 2 periods of high cone production by black spruce, 1996 and 1999 (mast years), separated by 3 years. Thus, the population of the Muskuchii hills may be fluctuating in accordance with mast years of black spruce, but more studies are needed to test this hypothesis. Determining the diet of southern red-backed voles in the black spruce forests as well as the experimental manipulation of food may prove useful to tease apart causes from effects in their population dynamics (Sinclair et al. 1988).

Predation has often been identified as the main cause of cyclic dynamics in small rodents, especially in Fennoscandia. Predators such as ermine and weasels (*Mustela* spp.), that specialize on small rodents, show strong numerical and functional responses to their prey abundance. This delayed response brings both predator and prey populations in a fluctuating tandem (Gilg et al. 2003). Johnson et al. (2000) showed that several populations of ermine were characterized by cyclic dynamics and argued that it may be related to the dynamics of its prey, which includes southern red-backed voles. However, predation by mustelids is not always a causal factor in vole population cycles (Graham and Lambin 2002). Cheveau et al. (2004) provided evidence that the irruptions of the boreal owl (*Aegolius funereus*), which is a specialist of small mammals, depended on the presence of abundant populations of small mammals. The high regularity of boreal owl irruptions may have been indicative of cyclic dynamics of southern red-backed voles. Other studies show similar regular fluctuations of owls (Côté et al. 2007; Bowman et al. 2010; Graves et al. 2012). Further studies

Table 1.—Autocorrelation (*r*) and autoregressive (β) coefficients with their respective standard errors (*SE*) estimated for the Muskuchii hills southern red-backed vole (*Myodes gapperi*) population in the black spruce and jack pine forest sites. Estimates in bold indicate that the 95% confidence interval did not include 0.

Site	Analysis	Parameter	Estimate	*SE*	Low 95% *CI*	High 95% *CI*
Black spruce	Autocorrelation	$r_{t, t+1}$[a]	0.08	0.41	−0.72	0.88
		$r_{t, t+2}$	**−0.78**	**0.25**	**−1.27**	**−0.29**
		$r_{t, t+3}$	0.02	0.39	−0.74	0.78
		$r_{t, t+4}$	**0.45**	**0.15**	**0.16**	**0.74**
		$r_{t, t+5}$	−0.23	0.34	−0.90	0.44
	Autoregressive	β_0[b]	**3.21**	**0.56**	**2.11**	**4.31**
		β_1[c]	**−1.03**	**0.21**	**−1.44**	**−0.62**
		β_2[d]	**−0.98**	**0.19**	**−1.35**	**−0.61**
Jack pine	Autocorrelation	$r_{t, t+1}$	−0.09	0.41	−0.89	0.71
		$r_{t, t+2}$	**−0.81**	**0.29**	**−1.38**	**−0.24**
		$r_{t, t+3}$	0.05	0.58	−1.09	1.19
		$r_{t, t+4}$	**0.99**	**0.37**	**0.26**	**1.72**
		$r_{t, t+5}$	0.01	0.95	−1.85	1.87
	Autoregressive	β_0	**1.92**	**0.45**	**1.04**	**2.80**
		β_1	**−1.07**	**0.31**	**−1.68**	**−0.46**
		β_2	**−0.78**	**0.26**	**−1.29**	**−0.27**

[a] $r_{t, t+i}$ = correlation between the abundance of year $t + i$ and year t.
[b] β_0 = intercept of the regression.
[c] β_1 = direct density dependence coefficient.
[d] β_2 = delayed density dependence coefficient.

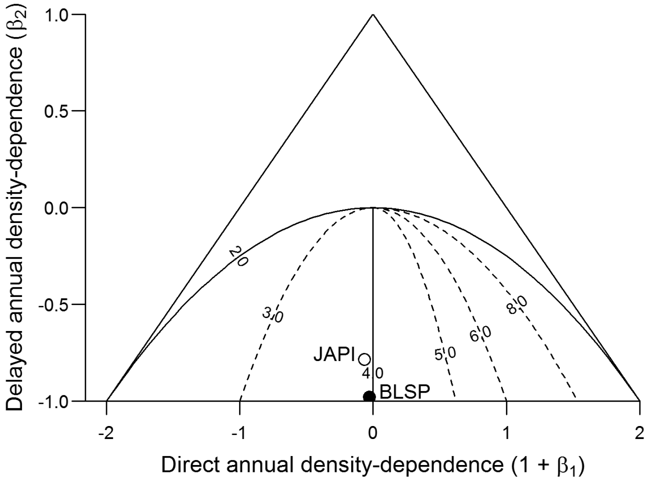

Fig. 2.—Phase plane diagram showing the coefficients for direct annual density dependence (β_1) and delayed annual density dependence (β_2) for the Muskuchii hills southern red-backed vole (*Myodes gapperi*) population in black spruce (BLSP; black circle) and jack pine (JAPI; white circle) forest sites.

are thus needed to clarify the relationship between the population dynamics of predators and southern red-backed voles, for instance, using experimental manipulation of predation (Salo et al. 2010).

One possible statistical caveat of our study is that even though we sampled southern red-backed voles during 9 years, it was not enough to conduct spectral analyses (Henttonen et al. 1985). Indeed, this type of model does not perform well under the restriction of a low number of years (< 15 years—Gruyer et al. 2008; Boonstra and Krebs 2012). However, the 2 almost-identical fluctuations of abundance and the strong statistical support by the autocorrelation and autoregressive analyses corroborate the cyclicity hypothesis for the red-backed vole population of the Muskuchii hills.

The southern red-backed vole population of the Muskuchii hills was characterized by cyclic dynamics between 2001 and 2009, with low phases in 2001, 2004–2005, and 2008–2009. Although it is possible that this short time frame may have coincided with 2 exceptionally well-defined cycles, northern owl irruptions appear to be in phase with such 4-year patterns at least over the last 50 years (1968—Catling 1972; 1984, 1988, and 1992—Cheveau et al. 2004; 1996 and 2000—Cheveau et al. 2004; Côté et al. 2007; 2004—Côté et al. 2007). Taken together, these results substantiate cyclic dynamics of southern red-backed vole populations in the northeastern boreal forests of North America.

ACKNOWLEDGMENTS

Financial support was provided by Natural Sciences and Engineering Research Council of Canada and Fonds Québécois de la Recherche sur la Nature et les Technologies. The Centre for Forest Research and the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management provided logistical support. We thank R. Julien, D. Charron, M.-H. Longpré, and the numerous field assistants for their logistical support and M. J. Mazerolle for the statistical support.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—R code for the statistical analyses of the population cycles.

Supporting Information S2.—Zip file containing all data files used in the R code.

Supporting Information S3.—Results from the spatially explicit capture–recapture analyses.

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Submitted 2 September 2014. Accepted 22 December 2014.

Associate Editor was Chris R. Pavey.