Cyclic dynamics of eastern Canadian ermine populations

Donald R. Johnson, Bradley J. Swanson, and Judith L. Eger

Abstract: Based on partial autocorrelation analysis, 20 ermine (*Mustela erminea*) populations in Manitoba, Ontario, and Quebec demonstrated cyclic dynamics characterized by a latitudinal gradient of decreasing first-order feedback and increasing negativity of second-order feedback. Most of these populations exhibited three cyclic peaks and a 10-year interval of noncyclic dynamics during the sampling period (1915–1940). Changes in ermine density probably reflected those in the density of microtine rodents, their primary prey. Analysis of the limited number of long-term lemming and vole series from boreal North America indicated a latitudinal gradient in cyclic dynamics similar to that of microtine rodent populations in northern Europe. Complex geographic and temporal variation in ermine population dynamics, including cyclic, noncyclic, and shifting patterns of density change, supports the specialist–generalist hypothesis of predator–prey interaction at temperate latitudes.

Résumé : D'après une analyse d'autocorrélation partielle, 20 populations d'Hermines (*Mustela erminea*) du Manitoba, de l'Ontario et du Québec ont une dynamique cyclique caractérisée par un gradient latitudinal des rétroactions de premier ordre et une négativité croissante des rétroactions de second ordre. La plupart de ces populations ont subi trois sommets cycliques et un intervalle de 10 ans de dynamique non cyclique au cours de la période d'échantillonnage (1915–1940). Les fluctuations de la densité des hermines reflètent probablement celles des rongeurs microtinés, leurs proies de prédilection. L'analyse du petit nombre de séries à long terme de lemmings et de campagnols de la zone boréale nord-américaine indique l'existence d'un gradient latitudinal de la dynamique des cycles semblable à celui qui prévaut chez les populations de rongeurs microtinés du nord de l'Europe. La variation géographique et temporelle complexe dans la dynamique des populations d'hermines, patterns cycliques, non cycliques ou fluctuants des changements de densité, appuie l'hypothèse de la prédation spécialiste–généraliste au cours des interactions prédateurs–proies aux latitudes tempérées.

[Traduit par la Rédaction]

Introduction

Field studies of the least weasel (*Mustela nivalis*) and stoat (*M. erminea*, the ermine of North America) have provided a significant part of the empirical data upon which the specialist–generalist hypothesis of predator–prey interaction was formulated (e.g., Hanski et al. 1991). The least weasel is a specialist predator in that a few species of microtine rodents provide the bulk of its diet. In contrast, the larger ermine is a " semi-generalist" (Korpimäki et al. 1991), taking a wider variety of prey. Although there is strong interaction between specialist predators and their favored prey, generalists are less affected by changes in the density of individual prey species because of their ability to switch to alterative food sources. However, the stoat is specialist predator at higher latitudes in Fennoscandia (Norway, Sweden and Finland), where the number of prey species is limited (Hanski and Henttonen 1996).

The specialist–generalist hypothesis predicts that mustelid predators produce the multi-annual cycles of microtine rodent populations at higher latitudes, where generalist predators are rare. Cyclic changes in density of specialist predator populations are dampened at temperate latitudes, where the dynamics of prey species are stabilized by a diverse community of avian and mammalian generalist predators (Hanski et al. 1991; Korpimäki et al. 1991).

In contrast to the abundant data from northern Europe, investigation of the interaction between small mustelids and microtine rodents in boreal North America has been limited. An analysis of the ermine time series representing Hudson's Bay Company returns from all of Canada (1848–1909) showed no evidence of periodicity (Finerty 1980). However, Finerty proposed that most ermines were taken in forested areas, where major prey populations were presumably noncyclic. He suggested that an analysis of ermine dynamics at a regional scale would prove useful.

In this paper we (*i*) investigate the density-dependent structure of eastern Canadian ermine populations, (*ii*) evaluate dynamics at the local level (using time series from individual fur posts) and regional level (using combined local series), (*iii*) describe latitudinal variation in cyclicity and shifts between stable and cyclic dynamics, and (*iv*) compare the dynamics of these ermine populations with those predicted by the specialist–generalist hypothesis.

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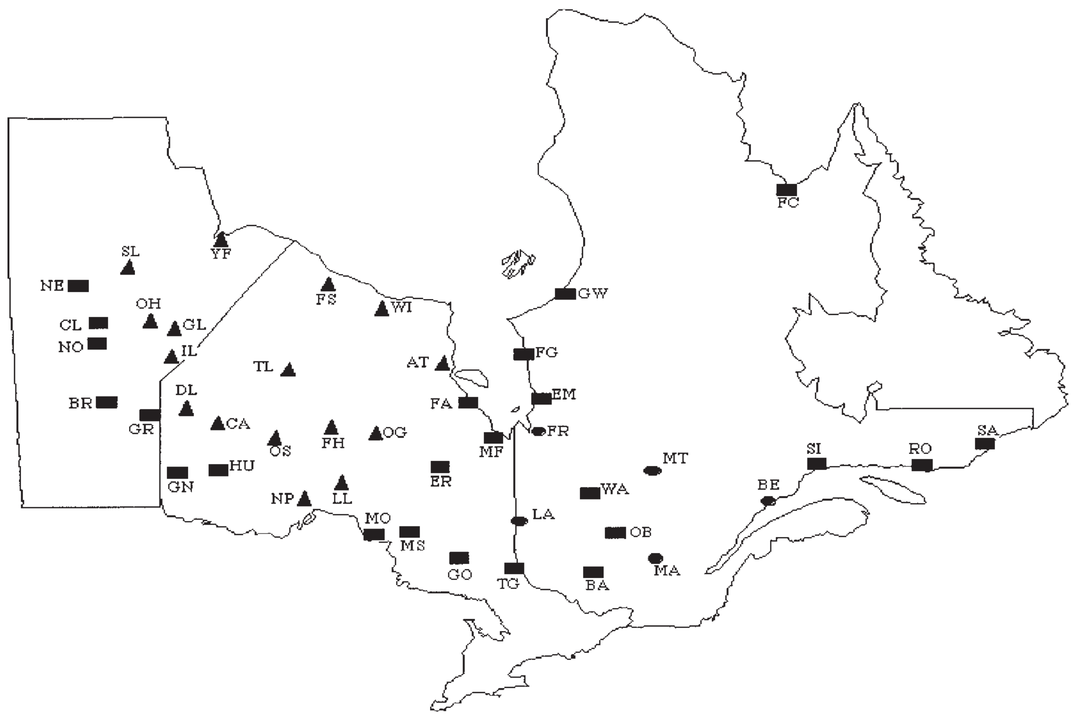
D.R. Johnson[1] and B.J. Swanson. College of Natural Resources, University of Wisconsin, Stevens Point, WI 54481, U.S.A.
J.L. Eger. Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada.

[1]Author to whom all correspondence should be sent at the following address: Department of Biological Sciences, University of Idaho, Moscow, ID 83844, U.S.A. (e-mail: drjcda@earthlink.net).

Fig. 1. Density-dependent structure of ermine populations at 45 Hudson Bay Company fur-trading posts in eastern Canada. A solid circle denotes direct density dependence; a solid triangle denotes delayed density-dependence; and a solid rectangle indicates that the series is nonstationary, lacks a density-dependent structure, or is abbreviated in length. Posts are designated as follows: AT, Attawapiskat; BA, Barriere; BE, Bersimis; BR, Beren's River; CA, Cat Lake; CL, Cross Lake; DL, Deer Lake; EM, Eastmain; ER, English River; FA, Fort Albany; FC, Fort Chimo; FG, Fort George; FH, Fort Hope/Lansdowne House; FR, Fort Rupert/Nemiscau; FS, Fort Severn; GL, God's Lake; GN, Grassy Narrows/Minaki; GO, Gogama; GR, Little Grand River; GW, Great Whale River; HU, Hudson; IL, Island Lake; LA, La Sarre; LL, Long Lake; MA, Manuan; MF, Moose Factory; MO, Mobert; MS, Missinabi; MT, Mistassini; NE, Nelson House; NP, Nipigone House/Nipigon Post; NO, Norway House; OB, Obedjiwan; OG, Ogoki; OH, Oxford House; OS, Osnaburgh House; RO, Romaine; SI, Seven Islands; SL, Split Lake; SA, St. Augustin; TG, Temagami; TL, Trout Lake; WA, Waswanipi; WI, Winisk; YF, York Factory.



Methods

Harvest data from Hudson's Bay Company posts (Royal Ontario Museum Library and Archives, Record Group 85, Box 24) in Manitoba, Ontario, and Quebec (Fig. 1) were analyzed to determine the dynamics of ermine populations from 1915 to 1940. Although Company records make no distinction among species, ermines represent a large majority of the harvest. There is little overlap between the ranges of ermines and long-tailed weasel (*M. frenata*), a larger species that occurs only in the southernmost parts of these provinces (Simms 1979). We assumed that any mixed samples from the regions of sympatry had a minimal effect on estimates of ermine density, based on the synchronous cycling of ermines and long-tailed weasels in Alberta (Keith and Cary 1991). It is unlikely that significant numbers of a third species, the least weasel, were included in harvest data because of its reported low densities at temperate latitudes (Simms 1979).

We used partial autocorrelation at lags 1 (principal component (PAC) 1) and 2 (PAC2) to characterize density-dependent structure (Royama 1992). This method is conservative in that the strength of the negative feedback at lag 1 is underestimated because of the effects of reproduction (Berryman 1992), and detection of lag-2 feedback is reduced in shorter series, such as those evaluated here (Holyoak 1994). Nonstationary series and series lacking a density-dependent structure (significant PAC1 or PAC2 values) were excluded from the analysis. The selected series were ln-transformed and detrended using least-squares regression (Royama 1992); most series showed a significant positive trend. Harvest from a post that opened during the sampling period was combined with that of an adjacent established post if there was evidence of competition between them. Combined series are included in the list of posts given in Fig. 1. We estimated cycle amplitude as the standard deviation of the ln-transformed detrended series. Cycle length was not estimated because of an interval of noncyclic dynamics within most time series. Based on the lack of correlation between fur price (Monk 1981) and total ermine harvest from Ontario between 1920 and 1938 (r = 0.06, p = 0.8), we assumed that price variation had a negligible effect on harvest throughout the region.

We searched the literature for microtine rodent series from the boreal parts of North America in order to compare the dynamics of potential prey populations with those of ermines. Seven series were long enough to allow calculation of partial autocorrelations (Table 2). In studies where vole populations were sampled seasonally, we evaluated estimates of population size in fall. Rodent series containing zero data points were transformed as ln (x + 1).

Results

Of the 45 local ermine series evaluated (Fig. 1), 25 were excluded from the analysis because they lacked stationarity or density-dependent structure. Of the remainder, 18 series demonstrated shifts between cyclic and noncyclic dynamics and 2 series from adjacent posts in central Ontario were continuously cyclic (Fig. 2). Amplitude (r = 0.59, p < 0.001) and negativity of partial autocorrelation values at lag 2 (r = –0.42, p < 0.04) increased with latitude. Partial autocorrelations at lag 1 were inversely related to latitude (r = –0.63,

Fig. 2. Cyclic dynamics of ermine populations at Osnaburgh House (●) and Fort Hope/Lansdowne House (▲). Time series are standardized to a mean of zero and unit variance.

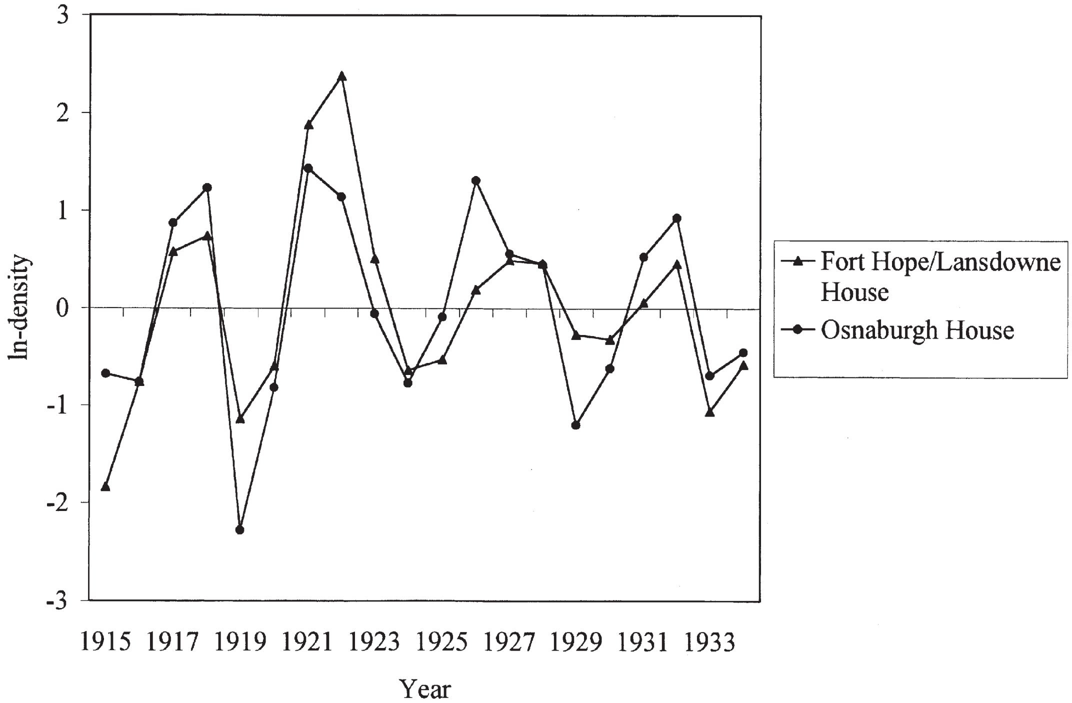


Table 1. Density-dependent structure of eastern Canadian ermine populations, based on records from Hudson Bay Company (HBC) posts.

HBC post[a]	Latitude (°N)	Series length (years)	Amplitude[b]	PAC1	PAC2
YF	57.0	25	1.08	0.19	–0.53*
SL	56.2	25	0.93	0.10	–0.51*
WI	55.3	19	0.90	0.30	–0.61*
FS	55.0	20	1.07	0.19	–0.46*
OH	54.9	25	0.80	0.15	–0.57*
GL	54.7	26	0.87	0.20	–0.57*
IL	53.9	26	0.98	0.15	–0.59*
TL	53.8	20	1.00	0.24	–0.58*
AT	52.9	20	0.77	0.26	–0.63*
DL	52.1	20	1.13	0.17	–0.59*
CA	51.7	16	0.78	0.22	–0.54*
FH	51.5	19	0.67	0.29	–0.62*
FR	51.3	25	0.72	0.43*	–0.18
OS	51.1	20	0.59	0.07	–0.70*
MT	50.4	25	0.72	0.50*	–0.16
LL	49.8	20	0.67	0.30	–0.51*
NP	49.2	20	0.60	0.11	–0.54*
BE	49.0	25	0.86	0.61*	0.11
LA	48.8	26	0.75	0.60*	0.04
MA	47.9	26	0.86	0.60*	–0.25
Combined populations			0.57	0.32	–0.61*

Note: PAC1 and PAC2 show partial autocorrelation at lags 1 and 2; *, $p < 0.05$.
[a]Posts are identified in Fig. 1.
[b]Calculated as the standard deviation of the ln-transformed detrended series.

$p < 0.003$). The regional time series, generated as the mean annual harvest from the 20 local series, demonstrated nonsignificant first-order feedback and significant negative second-order feedback (Table 1). The regional series and the majority of local time series exhibited shifts in dynamics, with cyclic peaks in 1917 and 1921, an interval of stability

Fig. 3. Dynamics of 20 combined local series demonstrating density-dependent structure. Time series are standardized to a mean of zero and unit variance.

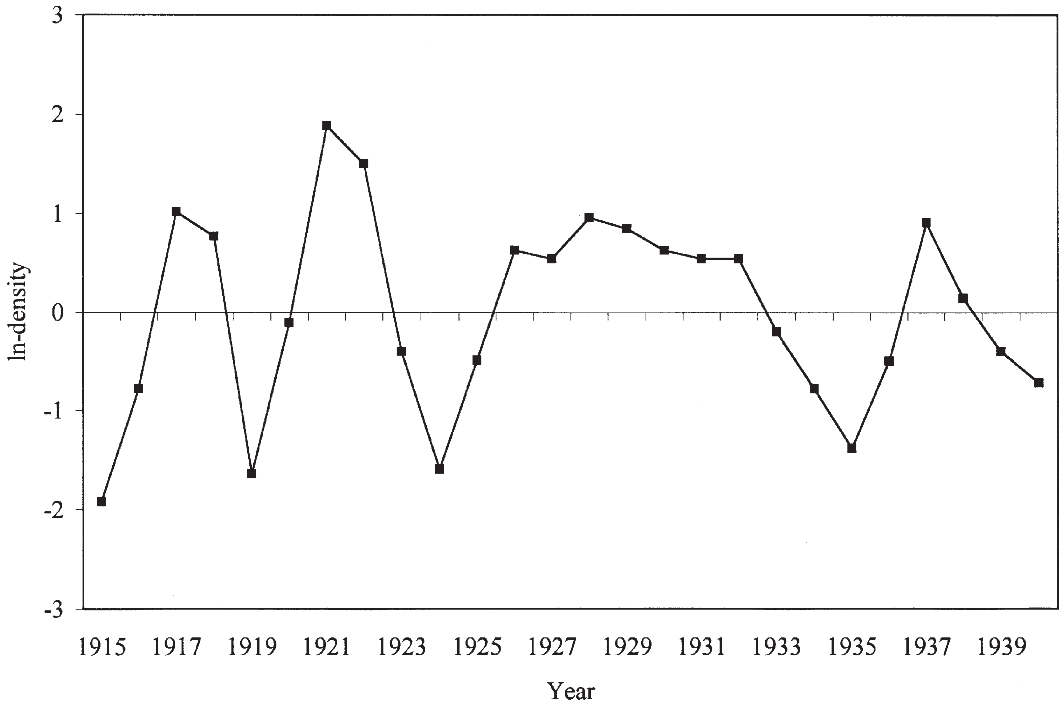


Table 2. Density-dependent structure of boreal rodent populations.

	Region	Latitude (°N)	Series length (years)	Amplitude[a]	PAC1	PAC2	Reference
Lemmus trimucronatus	Alaska	71	19	1.31	–0.2	–0.7*	Schultz 1969
Clethrionomys rutilis	Yukon	61	13	1.01	0.05	–0.61*	Gilbert and Krebs 1991
Dicrostonyx groenlandicus	Manitoba	59	13	1.48	–0.07	–0.55	Shelford 1943
Microtus pennsylvanicus	Manitoba	50	14	1.29	0.5	–0.24	Mihok et al. 1985
Clethrionomys gapperi	Manitoba	50	14	0.62	0.05	–0.18	Mihok et al. 1985
	Minnesota	48	13	0.92	–0.06	–0.18	Krefting and Ahlgren 1974
	Ontario	46	36	0.84	0.36*	0.15	Fryxell et al. 1998

Note: PAC1 and PAC2 show partial autocorrelation at lags 1 and 2; *, $p < 0.05$.
[a]Calculated as the standard deviation of the detrended ln-transformed detrended series.

from 1925 to 1934, and a return to a cyclic pattern with a peak in 1937 (Fig. 3).

Microtine rodents represent a major food source for small mustelids in North America (e.g., Maher 1967; Simms 1979). Meadow voles (*Microtus pennsylvanicus*) and southern red-backed voles (*Clethrionomys gapperi*) are the most common microtine species in eastern Canada. Other potential microtine prey include the eastern heather vole (*Phenacomys ungava*), bog lemmings (*Synaptomys borealis* and *Synaptomys cooperi*), and rock vole *Microtus chrotorrhinus*). The range of tundra-inhabiting collared lemmings (*Dicrostonyx groenlandicus*) extends into the northern parts of Manitoba, and *Dicrostonyx hudsonicus* occurs in northern Quebec. A geographic gradient in vole dynamics like that found in northern Europe (Turchin and Hanski 1997) is indicated by the correlation of latitude with negativity of partial autocorrelation values (PAC1, $r = -0.65$, $p = 0.11$; PAC2, $r = -0.92$, $p < 0.01$) but not with amplitude ($r = 0.57$, $p = 0.18$). The limited numbers of series reduced the significance of these correlations (Table 2). In the one instance where local predator and prey populations were sampled simultaneously, the 1937 peak in a short ermine series from Fort Churchill, Manitoba (latitude 59°N), lagged by 1 year the peak in the lemming population as reported by Shelford (1943).

Discussion

Although Royama (1992, p. 73) emphasized the vulnerability of linear models to overinterpretation, there is empirical evidence supporting our assumption that the density-dependent structure of specialist predator populations reflects that of their major prey. For example, partial autocorrelations of a least weasel time series (PAC1 = –0.46, PAC2 = –0.76; $p < 0.02$) and that of the local *Microtus* sp. population (PAC1 = –0.4, PAC2 = –0.76; $p < 0.02$) are nearly identical (calculated from Fig. 2 of Hanski et al. 1993).

We expected ermine populations at Fort Chimo and Great Whale River to be strongly cyclic, given the presence of lemmings throughout the northernmost parts of Quebec (Elton 1942, p. 472). However, these series were nonstationary, precluding analysis of their dynamics. Other species of microtine rodents may be more common in the vicinity of these posts, especially at Great Whale River at the periphery of the lemming range.

Hanski and Henttonen (l996) described a shift from cyclic to noncyclic dynamics in microtine populations in northern Finland. Based on behavior and body size, they ranked species of the genera *Lemmus* and *Microtus* as superior competitors and species of *Clethrionomys* as inferior. Using mathematical models, they showed that both populations demonstrated regular, high-amplitude cycles during which the superior competitor was numerically dominant and both were noncyclic during periods when the inferior competitor maintained the greater density. We suggest that shifts between cycling and noncycling in the mean annual ermine harvest (Fig. 3) may indicate similar changes in local microtine-prey populations, especially those of the meadow vole and red-backed vole.

Ermine and microtine rodent dynamics in boreal North America are of interest in relation to the specialist–generalist hypothesis, which predicts a delayed response by specialist predators and a direct response by generalist predators to changes in prey density (Hanski et al. 1991). The strongly negative second-order feedback in the majority of local ermine series and the combined (regional) series (Table 1) conform to the predicted density-dependent structure of specialist predator populations. Secondly, there was a significant positive relationship between cyclicity and latitude in both ermine populations and their potential prey. Finally, there was both temporal and geographic variation in the dynamics of ermine populations, as was predicted for specialist predators at temperate latitudes.

These results confirm that ermine time series from local and regional areas differ in dynamics, as suggested by Finerty (l980). Using cluster analysis, Swanson and Johnson (l999) identified 3–4 regions of synchronous density change in 6 species of eastern Canadian furbearers, including the ermine. Regions of synchronous dynamics varied in size within and between species. Thus, time series based on the fur harvest from provinces or other large geographic regions may mask variation in the dynamics of the constituent populations.

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