

Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America

Marianne Cheveau, Pierre Drapeau, Louis Imbeau and Yves Bergeron

Cheveau, M., Drapeau, P., Imbeau, L. and Bergeron, Y. 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. – *Oikos* 107: 190–198.

Contrary to what is observed in Fennoscandia, it seems to be widely accepted that small mammals do not exhibit multi-annual population cycles in the boreal forest of North America. However, in the last thirty years, irruptions of vole predators such as owls have been reported by ornithologists south of the North American boreal forest. While such southerly irruptions have been associated in Fennoscandia with periods of low abundance of small mammals within their usual distribution range, their possible cyclic nature and their relationships to fluctuations in vole densities at northern latitudes has not yet been demonstrated in North America. With information collected from existing data-bases, we examined the presence of cycles in small mammals and their main avian predators by using temporal autocorrelation analyses. Winter invasions of boreal owls (*Aegolius funereus*) were periodic, with a 4-yr cycle in Québec. Populations of one species of small mammal, the red-backed vole (*Clethrionomys gapperi*), fluctuated periodically in boreal forests of Québec (north to 48°N). Boreal owls show invasion cycles which correspond to years of low density of red-backed voles, the main food item for this owl species. In addition, winter observations of northern hawk owls (*Surnia ulula*) and great gray owls (*Strix nebulosa*) south of their usual range increased in years of low density of red-backed voles. Our results suggest that a 4-yr population cycle exists in the eastern boreal forest of North America for voles and owls, which is very similar to the one observed in Fennoscandia.

M. Cheveau, P. Drapeau, L. Imbeau and Y. Bergeron, Dépt des Sciences Biologiques, Univ. du Québec à Montréal, C.P. 8888, Succursale Centre Ville, Montréal, Qc, Canada, H3C 3P8, and Chaire industrielle CRSNG, Univ. UQAT-UQAM en Aménagement Forestier Durable, Dépt des Sciences Appliquées, Univ. du Québec en Abitibi-Témiscamingue, 445 Boulevard de l'université, Rouyn-Noranda, Qc, Canada, J9X 5E4 (cheveau.marianne@courrier.uqam.ca).

Small mammals, and voles in particular, are known for their regular multi-annual population fluctuations, with a periodicity between 3 to 7 years documented in several countries (e.g. Russia, Japan, Finland and Scotland; Stenseth 1999, Klemola et al. 2002, France; Salamolard et al. 2000 and Switzerland; Weber et al. 2002). However, most of the studies showing the presence of such cycles were done in Fennoscandia (Hörnfeldt 1978, Hansson and Henttonen 1985, Hanski et al. 1993, Norrdahl and Korpimäki 2002). In this area, north of 60°N, abundance

cycles of microtine voles generally increase in duration (3 to 5-yr) and amplitude as a function of latitude. Conversely, these cycles are not observed further south (Hanski et al. 1991). A likely explanation of this general latitudinal gradient lies in the geographic distribution of microtine vole specialist predators, which would be responsible for the regular multi-annual cyclic dynamic of their prey. Indeed, Turchin and Hanski (1997) have shown that specialist predators occur in greater proportion in the northern part of Fennoscandia, whereas

Accepted 1 March 2004

Copyright © OIKOS 2004
ISSN 0030-1299

generalist predators generally dominate further south. The greater proportion of generalist predators in more southern localities is assumed to stabilize rodent populations in these regions, because of their possibility of having several alternative prey species (Hanski et al. 1991).

Among vole specialist predators found in Fennoscandia, two functional categories at the ends of a continuum have often been recognized: resident specialists (small mustelids) have weak dispersion capacities, and thereby are assumed to drive the predator–prey cycle, while nomadic specialists (raptors and owls) can move over great distances in response to varying prey availability. In the case of some owl species restricted to the boreal zone (e.g. boreal owl), their winter irruptions south of the boreal forest are well documented in Fennoscandia (Mysterud 1970, Korpimäki 1986, Sonerud et al. 1988), where they happen during periods of low abundance of small mammals within their usual distribution range (Mikkola 1983). In this case, owls react to a lack of prey in the north by massively moving to the south, where small mammal cycles are non-existent. Such large scale movement patterns can thus be good indicators of the population fluctuations of small mammals in the north.

Contrary to Fennoscandia, far less is known in North America about the abundance cycles of small mammal populations. Lemming cycles in the tundra are well documented (Pitelka et al. 1955, Framstad et al. 1993, Wilson et al. 1999, Turchin et al. 2000), as are those of snowshoe hares and lynx in the boreal forest (Elton and Nicholson 1942, Krebs et al. 2001). However, it has become largely accepted that most of the species of voles in North America do not show regular cycles, in boreal forest species (*Clethrionomys gapperi*) as well as in tundra species (*Clethrionomys rutilus*, which is thought to be cyclic in Fennoscandia; Hansson and Henttonen 1985, Boutin et al. 1995). Accordingly, Turchin and Hanski (1997) argue that fluctuations in the abundance of small mammals exist in North America but periodicity does not. Mostly because hares replace voles as the predominant herbivore in the system, it has been suggested that specialist predators in North America are larger bodied and prey mostly upon hares instead of voles. Consequently, it has been proposed that the vole cycles of Fennoscandia are replaced by snowshoe hare cycles in North America (Hansson and Henttonen 1985, Boutin et al. 1995).

Although one third of the world's boreal forest is found in Canada (World Resources Institute 2000), it has been relatively little studied in terms of small mammal population dynamics. The studies conducted so far were fragmentary and have been most often conducted south of the boreal forest zone, predominantly in mixed to deciduous forests. As it is the case in the southern part of Fennoscandia, these studies suggest

an absence of regular cycles (Grant 1976, Brooks et al. 1998, Fryxell et al. 1998). To our knowledge, no long-term study appears to have been done to date in the northeastern part of the boreal forest, which has a primarily coniferous forest cover (north of 48°N). This begs the question whether or not it is simply a lack of knowledge which leads us to think that no regular small mammal population cycles occur in eastern boreal forests of North America, especially when the resident specialist predators present (small mustelids) are similar to those associated to multi-annual population cycles of voles in Fennoscandia. Indeed, Johnson et al. (2000) have suggested that ermine (*Mustela erminea*) populations show fluctuations in abundance for which amplitude increases with latitude in eastern North America. Using a limited number of published long-term data-sets on different species of small mammals from boreal North America, these authors were the first to suggest that a latitudinal gradient in cyclic dynamics was occurring in this region, similar to that of microtine rodent populations in northern Europe. In agreement with this hypothesis, winter owl irruptions south of the boreal forest have already been observed by ornithologists in North America (Catling 1972, Bondrup-Nielsen 1978). Although these irruptions of nomadic specialists could possibly be the result of a phenomenon similar to that observed in northern Europe, the possible cyclic nature of these irruptions in North America has however yet to be demonstrated.

In this paper, we formulate the hypothesis that small mammal abundance cycles exist in the coniferous boreal forest of eastern North America, similar to those observed in Fennoscandia. To test this hypothesis, we used a comparative approach based on the analysis of available ornithological and small mammal data-bases in order to 1) evaluate the cyclic nature of owl irruptions and small mammal population fluctuations, and 2) measure the quantitative associations between these two data-sets.

Material and methods

Data-bases

Large data-bases of bird sightings are compiled each year using the observations of amateur ornithologists in Canada as well as in the United States. Such sources of information have already been used to monitor long-term fluctuations in bird populations (Cyr et al. 1997, Droege et al. 1998, Koenig 2001).

In this study, two such data-bases were used. The first was compiled from the journal *American Birds* (1971–1994), renamed *National Audubon Society Field Notes* (1994–1997), then *American Birding Association Field Notes* (1998), and finally *North American Birds* (1999–2001). This journal publishes the observations of ama-

teur ornithologists for all regions of North America each season. We chose to monitor three owl species that prey mostly on small mammals and whose nesting range is almost entirely within the boreal forest: boreal owl (*Aegolius funereus*) (BO; Hayward and Hayward 1993), northern hawk owl (*Surnia ulula*) (NHO; Duncan and Duncan 1998) and great gray owl (*Strix nebulosa*) (GGO; Bull and Duncan 1993). As a result of snow accumulation throughout the winter, it is in this season that available food becomes limiting. We therefore collected only winter observations (October to March), for all regions of eastern North America located south of the boreal forest (Atlantic Provinces, Québec, Ontario, New England, Hudson-Delaware, Western Great Lakes) (Fig. 1).

The second data-base, the Étude des populations d'Oiseaux du Québec (EPOQ; Larivée, 2001), is a compilation of field observations made by amateur ornithologists on checklists in the province of Québec, Canada. This data-base was analyzed for the same three owl species, in winters (October to March) from 1971 to 2001 for the entire Québec region. In this data-base, only one bird per location per winter was retained in order to avoid recording the same individual several times, notwithstanding elapsed time between two observations made the same winter. Furthermore, the number of owls recorded over the years was calibrated with regards to the observation effort, by considering the entire number of checklists filled by birders every winter. The EPOQ data-base is therefore more reliable than American Birds data-base, because it accounts for the observation effort.

On the other hand, the EPOQ data-base covers a smaller geographical area. Furthermore, both data-bases provide a rough estimate of owl abundance patterns, and do not cover systematically the land base, birders activities being concentrated in inhabited areas. However, they should allow general trends to be identified in the annual variations of the monitored species.

Small mammal population trends were analyzed with the data-base of the Atlas des Micromammifères du Québec (AMQ) (Société de la Faune et des Parcs du Québec, 2000). This data-base compiles small mammal surveys, done by various organizations, for various purposes, within the province of Québec. The data-base combines studies which were not intended to quantify cycles of abundance, which used different sampling methods and which had varying capture periods (from May to November). Despite these limitations, to our knowledge, this data-base contains the best available long-term information on the abundance of small mammals in north-eastern boreal forests of North America. Only four species provided sufficient data to be analyzed: red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), deer mouse (*Peromyscus maniculatus*) and masked shrew (*Sorex cinereus*). We selected only surveys which were done in forest ecosystems, north of 48°N, and for which sampling effort (number of trap-nights) was known. We were thus able to determine the summer abundance (capture rate), for all of boreal Québec, for each species for each year. We were able to assemble a continuous data-base for 1990 to 2000 only.

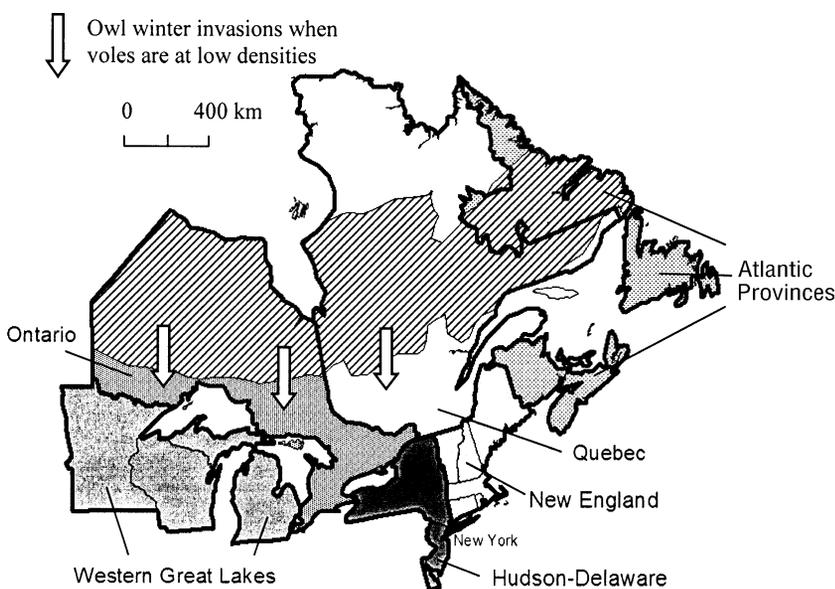


Fig. 1. Map of eastern North America, viewing the different study regions (in white and various gray) and localization of the boreal forest (hatched) (small mammals are in the boreal forest and owl invasions are south of the boreal zone). Limit of boreal forest is limit of black spruce forest based on Anseau et al. (1996).

Statistical analyses

The normality of the data originating from the three data-bases was verified using the Kolmogorov–Smirnov test. We were able to calculate the correlation (Pearson's or Spearman's r) between the ornithological data-bases for each owl species, first for the Québec region only (EPOQ and Québec region in American Birds), and then between Québec (EPOQ) and eastern North America (American Birds, all regions together). Secondly, temporal autocorrelation analyses were done for each species, in order to detect a potential periodicity in the observations (Turchin and Taylor 1992). Because of the short length of the time series, temporal autocorrelation analyses could not be done for small mammal data. However, the correlation between the summer abundance of the different species of small mammals and the number of observations of the three owl species was calculated performing a one-year time lag for the small mammal data. Small mammals were captured during summer (ex.: summer 1998), whereas the owls were observed the following winter (ex.: winter 1998–1999 is named winter 1999). This allowed us to evaluate the numerical response of the owls to the current abundance of small mammals, through the indicative knowledge of their abundance the preceding summer.

A cross correlation was calculated between the abundance of owl species (EPOQ) and the abundance of small mammals. This analysis compares two time series and determines with which time lag the correlation between the two is strongest. This allowed us to hypothesize which variable controls the other (Legendre and Legendre 1998). Thus, it will be possible to determine if a low phase in a cycle of small mammals drives southern owl irruptions, and if this is the case, with what time lag is the response observed. All statistical analyses were done using SPSS 10.0 (SPSS Institute Inc. 1999).

Results

Owls

During the period surveyed (1971–2001), a total of 6691 owls (1609 NHO, 3953 GGO and 1129 BO) were recorded in the winter reports of American Birds. In the EPOQ data-base, the minimum number of owls observed was 1499 (645 NHO, 647 GGO and 207 BO), for 134 413 checklists compiled during winters from 1971 to 2001 (Table 1).

The observations for the Québec region which are compiled in American Birds are highly correlated to those recorded in EPOQ, after weighting the data with the number of checklists filled (BO: $r = 0.465$, $P = 0.004$; NHO: $r_s = 0.819$, $P < 0.001$; GGO: $r_s = 0.892$, $P < 0.001$). In addition, observations from EPOQ are correlated to

Table 1. Number of records per winter (October to March) in EPOQ data-base. October to December records for one year are regrouped with next winter year (January to March; ex: October 1998 to March 1999 are named winter 1999). Owls number (NHO: northern hawk owl, GGO: great gray owl and BO: boreal owl) is a minimum number of individuals observed each winter, because only one bird per location per winter has been counted, notwithstanding time between observations.

Winters	Number of checklists	Owl number		
		NHO	GGO	BO
1971	697	9	2	1
1972	735	0	0	0
1973	782	1	8	2
1974	1137	12	7	3
1975	1294	1	0	2
1976	1666	1	2	1
1977	1720	8	2	6
1978	1841	4	2	4
1979	2309	10	45	2
1980	2016	5	2	8
1981	2483	5	1	3
1982	2575	16	2	0
1983	3824	7	0	4
1984	3660	9	172	6
1985	5432	7	2	11
1986	4395	3	5	2
1987	4535	8	1	6
1988	5371	42	37	11
1989	5718	28	15	13
1990	6563	4	1	2
1991	7064	42	11	6
1992	7602	139	91	15
1993	7372	51	15	22
1994	6493	6	1	4
1995	6837	6	1	1
1996	8401	11	80	15
1997	7968	98	98	23
1998	6768	13	2	9
1999	5510	4	1	3
2000	6107	1	5	6
2001	5538	94	36	16

those for all of eastern North America (American Birds, all regions together) (BO: $r_s = 0.537$, $P = 0.001$; NHO: $r_s = 0.715$, $P < 0.001$; GGO: $r_s = 0.813$, $P < 0.001$). This correspondence between EPOQ (Québec region only) and American Birds (all eastern North America) is a good indication that the information contained in American Birds is reliable, in spite of the absence of effort data.

Fluctuations in abundance were observed for the three owl species, in all regions of eastern sub-boreal North America (American Birds). However, it is in Ontario, Québec and Western Great Lakes regions that these fluctuations were the greatest. At least four strong winter irruptions, which are relatively synchronous for the three owl species (1988–89, 1992–93, 1996–97 and 2001), have occurred south of the boreal forest in recent years (Fig. 2). Before 1985, irruptions of the three species were less synchronous. During the first 15 years, the northern hawk owl was mostly irregular and the great gray owl showed quite low numbers. However, irruptions of these three species of owls are positively correlated among species for eastern North America (American Birds)

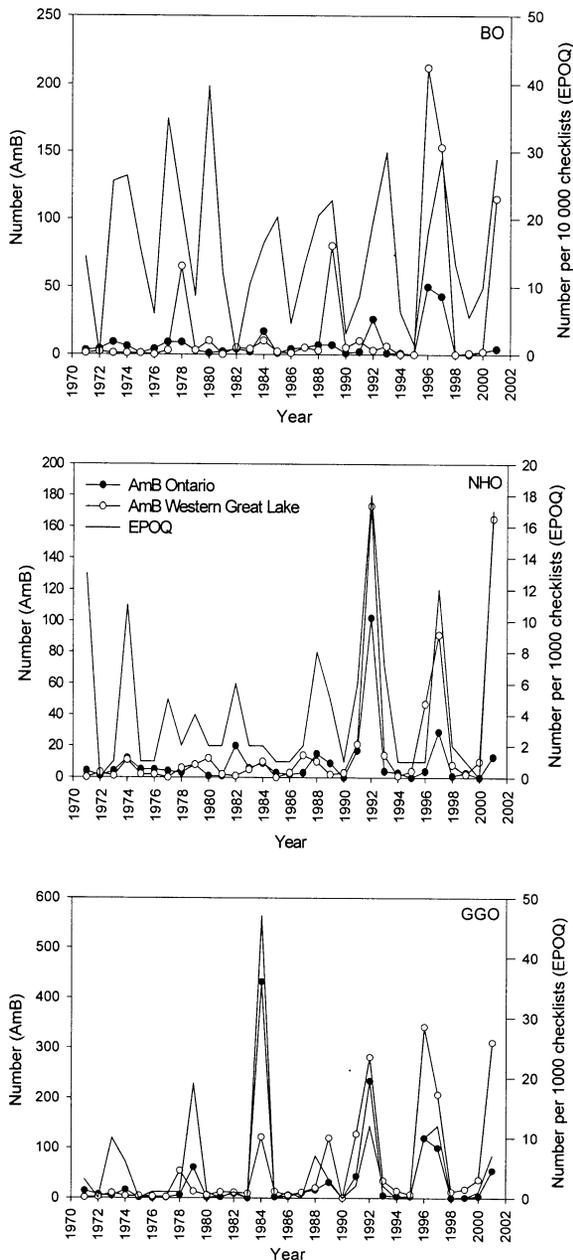


Fig. 2. Fluctuations in the numbers of owl observations (BO: boreal owl, NHO: northern hawk owl, GGO: great gray owl) by amateur ornithologists in different regions of eastern North America (Québec, Ontario, Western Great Lakes). The observations in EPOQ are weighted according to the number of checklists produced in each winter. AmB: American Birds data-base, EPOQ: Étude des Populations d'Oiseaux du Québec data-base.

(BO-NHO: $r_s = 0.751$, $P < 0.001$; BO-GGO: $r_s = 0.705$, $P < 0.001$; NHO-GGO: $r_s = 0.737$, $P < 0.001$), as well as in Québec (EPOQ) (BO-NHO: $r_s = 0.510$, $P = 0.002$; BO-GGO: $r_s = 0.497$, $P = 0.002$; NHO-GGO: $r_s = 0.523$, $P = 0.001$). Furthermore, for each owl species, the same fluctuation pattern is observed ($P < 0.05$) in the three

regions (Ontario, Québec, Western Great Lakes), except for the northern hawk owl which has a slightly different fluctuation pattern in Ontario than in Western Great Lakes ($P = 0.055$).

Temporal autocorrelations show that boreal owl has a significant irruption periodicity of 4 years, in Québec only (EPOQ) (lag=2: $r = -0.573$, $P = 0.001$; lag=4: $r = 0.444$, $P = 0.02$) (Fig. 3). The two other owl species do not show significant regular period, either from the EPOQ data-base or from the American Birds data-base (all $P > 0.05$).

Small mammals

The data-base consulted (AMQ) had 6729 recorded captures of small mammals for a total of 113930 trap-nights (Table 2). The summer abundance of small mammals (capture rate for 100 trap-nights) has varied a lot throughout the years, but the two peaks observed in red-backed vole abundance are consistent with the hypothesis that cyclic dynamic exist in boreal forest of Québec (Fig. 4). We saw three summers with low populations: 1992, 1996 and 2000, which were all followed by winters of owl irruptions. The other small mammal species do not seem to have a periodicity.

For Québec as a whole, the abundance of red-backed vole is inversely and significantly correlated to boreal owl observations (EPOQ; $r_s = -0.725$, $P = 0.009$), as well as to the great gray owl ($r_s = -0.782$, $P = 0.004$) and to the northern hawk owl ($r_s = -0.804$, $P = 0.003$). The abundance of red-backed vole, in Québec, is also significantly correlated to boreal owl observations in eastern North America (American Birds) ($r_s = -0.774$, $P = 0.003$), as well as to the great gray owl ($r_s = -0.629$, $P = 0.019$) and to the northern hawk owl ($r_s = -0.688$, $P = 0.01$). The other small mammal species had no significant correlations with any of these owls.

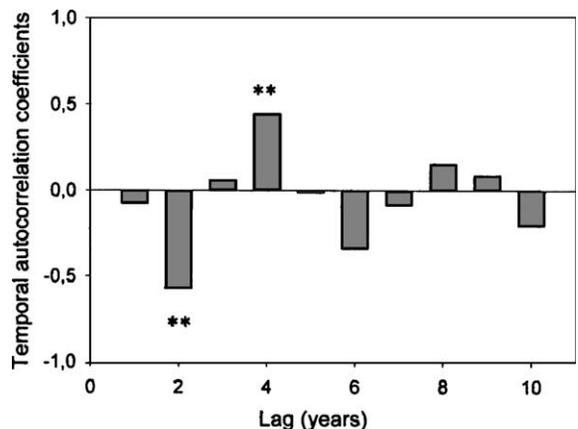


Fig. 3. Temporal autocorrelation coefficients (Pearson's r) at different time lag for weighted numbers of boreal owls (EPOQ) in Québec. ** $P < 0.05$.

Table 2. Number of studies compiled each year and total capture effort associated (number of trap-nights) in Atlas des Micromammifères du Québec data-base. Total capture numbers of the four species of small mammals per year is shown.

Years	Number of studies	Number of trap-nights	Red-backed voles	Deer mice	Meadow voles	Masked shrews
1990	2	8320	284	41	47	7
1991	5	11253	173	89	0	22
1992	4	24928	278	161	4	178
1993	4	11128	1114	5	30	45
1994	7	11806	334	221	9	54
1995	6	7715	207	203	6	180
1996	4	16777	96	49	0	62
1997	6	7746	311	245	10	63
1998	7	5918	612	74	1	72
1999	7	6088	546	244	241	308
2000	3	2251	34	4	48	17

The cross correlation between boreal owls (EPOQ) and red-backed voles was significantly strongest at lag = 0 ($r = -0.698$), indicating that both species fluctuated simultaneously, or at least with a time lag of less than a year. For the other two species of owls (EPOQ), the cross correlation analysis shows that no correlation was significantly strongest with any particular lag, between these species and the red-backed vole.

Discussion

Cyclic dynamic of owls and small mammals in eastern North America

Our results show that boreal species of owls make periodic irruptions in southern Québec, as well as in the entire sub-boreal zone of eastern North-America. These irruptions are synchronous among owl species.

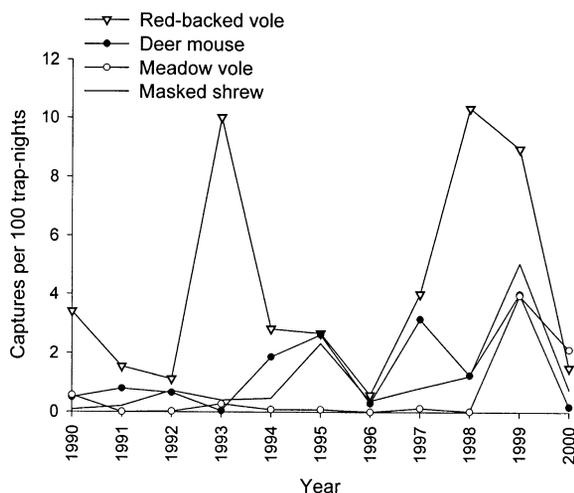


Fig. 4. Summer abundance (capture rate for 100 trap-nights) for four small mammal species (AMQ) north of 48°N in Québec.

The phenomenon of owl irruptions has been well studied in northern Europe and is indicative of fluctuations in the abundance of their prey. Indeed, the three species of owls studied are considered as nomadic specialist predators of small mammals in Fennoscandia, where their numerical fluctuations are known to follow those of voles (Mikkola 1983). Andersson (1980) has shown that it is more advantageous for a bird to adopt a nomadic strategy (movements of 100 km or more) when the abundance of its prey is cyclic. Boreal species of owls can therefore be considered as good indicators of fluctuations of small mammal abundance (Sundell et al. 2004).

Moreover, our results reveal that during the last ten years, the abundance of red-backed voles has fluctuated in Québec, and that there is a synchrony between their lowest abundance and the irruptions of the three species of owls, and particularly for boreal owl. This owl species shows regular 4-yr cycles in Québec and is strongly correlated to the abundance of red-backed voles for the 1990–2000 period. These results, although limited to a relatively short time series, also argue very strongly for the occurrence of population cycles in this small mammal species. Therefore, as opposed to other authors (Hansson and Henttonen 1985, Boutin et al. 1995) arguing that periodicity in small mammal abundance does not exist in North America, our results on winter owl irruptions in eastern North America suggest a small mammals population fluctuation pattern which is similar to that occurring in Fennoscandia, strongly supporting the hypothesis first set forth by Johnson et al. (2000).

Different responses of owls

The three species of owls seem to match the fluctuations of the red-backed vole, but only boreal owl has shown significant regular cycles in its irruptions. We suggest that the stronger cyclic pattern of this latter species may be largely explained by its size and its habitat preferences. Indeed, boreal owl is one of the smallest boreal owl predator, restricted to mature and old-growth forests (Gosse and Montevecchi 2001). These two characteristics limit its choice of potential prey. Its size limits it to very small animals such as voles, whereas its preferred habitat is dominated by one prey species in North America: the red-backed vole (Boos and Watt 1997). Hayward et al. (1993) showed that 80% of the diet of boreal owl consists of small mammals in North America, the majority of which are red-backed voles (*Clethrionomys gapperi*) and a further 10% of the diet derived from other species of voles (*Microtus* sp.).

In contrast to boreal owl, the northern hawk owl and the great gray owl, because of their larger size, have access to a greater number of prey species of various sizes. The northern hawk owl is opportunistic and therefore adapts its diet according to the abundance of

various prey (Rohner et al. 1995). In Fennoscandia, the most available prey during the nesting season are small mammals, and consequently the diet of northern hawk owls consists of more than 90% in voles. In winter, this percentage decreases and that of birds increases (Mikkola 1983). In Yukon, this owl species responds to combined density fluctuations of *Microtus* sp. and of juvenile snowshoe hares, which have 10-yr abundance cycles (Rohner et al. 1995). The great gray owl, which is a large owl species, eats only occasionally larger prey than voles (Mikkola 1983, Bull and Duncan 1993). In western North America, this owl eats species such as the pocket gopher (*Thomomys talpoides*), in proportion of their availability (Bull et al. 1989), but this prey species is absent from eastern North America.

In addition to their size, the larger two species of owls also hunt in open environments (Bull et al. 1988a, Gosse and Montevecchi 2001), where *Microtus* sp. are almost exclusively found, whereas red-backed voles (*Clethrionomys*) occur in the understory of mature forests (Banfield 1977). Their habitat use will therefore lead both owl species to consume more *Microtus* than *Clethrionomys*, compared to boreal owl (Bull et al. 1989, Rohner et al. 1995). Indeed, great gray owl seems to select preferentially *Microtus* sp. in any season, in Fennoscandia as well as in North America (Mikkola 1983, Bull and Duncan 1993).

Boreal owls respond to low prey density within their usual distribution range by moving towards the south (Korpimäki 1986). In Norway, Sonerud et al. (1988) have observed that their movements are longer during small mammal population lows than during peaks. Boreal owl seems to adopt a partial migration strategy, differing according to sex, age, and level of small mammal populations (Lundberg 1979, Korpimäki 1986). Females are more often nomadic (Hipkiss and Ellegren 2002), whereas males have greater advantage (rarity of nesting sites) and facility (better hunting efficiency) by protecting a territory surrounding a nesting site (Löfgren et al. 1986, Korpimäki et al. 1987). When prey populations are high, females and juveniles remain resident, or only travel short distances. When prey populations plummet, a proportion of females undertakes long migrations in search of areas where preys are more abundant, similarly to dispersing juveniles (Sonerud et al. 1988). The northern hawk owl seems to adopt a movement strategy similar to that of boreal owl, however it is less restricted in its choice of nesting sites (Byrkjedal and Langhelle 1986). The great gray owl seems to move, in Fennoscandia as well as in North America, over shorter distances than the northern hawk owl and boreal owl (Hildén and Helo 1981, Bull et al. 1988b).

However, we should bear in mind that in spite of the absence of clear periodicity of the northern hawk owl and the great gray owl, these two species still match the cyclic fluctuations of boreal owl, as it has already been

suggested (Hayward and Hayward 1993). They are thus affected by fluctuations in the red-backed vole population, but less than the boreal owl which has a more restricted diet. Perhaps, the lack of a clear pattern for the great gray owl may also be explained by the fact that this species still seems rare in eastern North America and Québec, with in this latter case very few confirmed nesting sites recorded to date (Gauthier and Aubry 1995).

Possible causes of small mammal cycles

The behavioral response of boreal owls to lack of food is immediate, and does not result in a time lag between the drop in prey populations and the migration movements (our data, Hörnfeldt 1978, Korpimäki 1985, Strann et al. 2002). This suggests that the owls are not the cause of small mammal cycles (Korpimäki and Norrdahl 1989, Norrdahl and Korpimäki 1995). Their nomadic behavior would instead have a stabilizing effect on prey populations (Korpimäki 1985), as would a generalist predator (Turchin and Hanski 1997).

In Fennoscandia, specialist mammalian predators such as ermine (*Mustela erminea*) and especially least weasel (*Mustela nivalis*) are considered the main drivers of vole cycles (specialist predator hypothesis; Korpimäki et al. 1991, Hanski et al. 1993, Korpimäki and Norrdahl 1998, Korpimäki et al. 2002). The generality of this hypothesis is, however, currently highly debated (Graham and Lambin 2002, Korpimäki et al. 2003, Lambin and Graham 2003, Oli 2003a, b).

Far less is known about these small mustelids in North America (Swanson and Johnson 1999, Johnson et al. 2000). Regardless that the vole cycles observed in eastern North America are linked or not to the predator specialist hypothesis, our results indicate that this portion of the boreal forest could be a fertile ground for testing this explanatory hypothesis with large-scale and long-term predator-manipulation experiments such as those conducted in other parts of the world (Korpimäki and Norrdahl 1998, Graham and Lambin 2002, Korpimäki et al. 2002). As suggested by Oli (2003a), this could help us evaluate if North American vole cycles in the boreal forest are caused or not by specialist mammalian predators.

To date, no study has detected the presence of regular cycles in the red-backed vole, which is widely distributed and well studied in North America (Banfield 1977). The majority of studies do not even consider the possibility of cycles for this species. Yet, in addition to results presented on ermines by Johnson et al. (2000), our results on boreal species of owls, and boreal owl in particular, appear to support that such cycles do occur in the boreal region of eastern North America. It is surprising that such an important phenomenon has

gone undetected. It is now timely to document the causes of these cyclic fluctuations in small mammal abundance in the boreal forest of eastern North America.

Increased knowledge of multi-annual population cycles in small mammals can also have important consequences in the assessment of sustainable forest management. For instance, the red-backed vole has been proposed as an indicator of old-growth forest conditions in the boreal forest of eastern North America (Génier and Bergeron 1996, McLaren et al. 1998, Potvin et al. 1999). Conclusions from studies documenting red-backed vole response to pre vs post-harvest treatments could be misleading if the cyclic changes in the density of its population are not considered. Conversely, vole cycles could be affected by the large-scale shift of the land base from naturally disturbed to a managed system that is occurring throughout the boreal ecosystem. Long-term studies of population dynamics of small mammals in natural and managed landscapes of North American boreal forests are thus greatly needed to assess these potential effects.

Acknowledgements – This study could not have been conducted without the keen observations of thousand of birders, who collected more than 130 000 daily observations, in the winter period during the last 30 years. More particularly, we acknowledge Jacques Larivée for extracting winter owl observations from the EPOQ data-base, used in our analyses. We also thank Robert Morin from Société de la Faune et des Parcs du Québec for giving access to the Atlas des Micromammifères du Québec data-base. We thank students from Pierre Drapeau laboratory and Hannu Pietiäinen for comments on previous version of this manuscript. Finally, we thank Patricia Wood for the English translation of an earlier draft of the manuscript. This project was funded by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, a Québec FCAR-Fonds Forestier programme d'Action Concertée grant, an industrial NSERC grant to Yves Bergeron, Norbord Industries Inc., and the Groupe de Recherche en Écologie Forestière interuniversitaire (GREFI).

References

Andersson, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. – *J. Anim. Ecol.* 49: 175–184.

Ansseau, C., Bélanger, L., Bergeron J.-F. et al. 1996. Écologie forestière. – In: *Ordre des ingénieurs forestiers du Québec, Manuel de foresterie*. Les Presses de l'Univ. Laval, pp. 133–279.

Banfield, A. W. F. 1977. Les mammifères du Canada. – Univ. of Toronto Press.

Bondrup-Nielsen, S. 1978. Vocalizations, nesting and habitat preferences of the boreal owl (*Aegolius funereus*) in North America. – M.Sc. Thesis, Univ. of Toronto, Canada.

Boos, J. D. and Watt, W. R. 1997. Small mammal habitat associations in the Lake Abitibi Model Forest of north-eastern Ontario. – Ontario Min. of Nat. Res., Northeast Science and Technology. TR-030.

Boutin, S., Krebs, C. J., Boonstra, R. et al. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada boreal forest. – *Oikos* 74: 69–80.

Brooks, R. T., Smith, H. R. and Healy, W. M. 1998. Small-mammal abundance at three elevations on a mountain in

central Vermont, USA: a sixteen-year record. – *For. Ecol. Manage.* 110: 181–193.

Bull, E. L. and Duncan, J. R. 1993. Great gray owl. – *Birds N. Am.* 41: 1–15.

Bull, E. L., Henjum, M. G. and Rohweder, R. S. 1988a. Nesting and foraging habitat of great gray owls. – *J. Raptor Res.* 22: 107–115.

Bull, E. L., Henjum, M. G. and Rohweder, R. S. 1988b. Home range and dispersal of great gray owls in northeastern Oregon. – *J. Raptor Res.* 22: 101–106.

Bull, E. L., Henjum, M. G. and Rohweder, R. S. 1989. Diet and optimal foraging of great gray owls. – *J. Wildl. Manage.* 53: 47–50.

Byrkjedal, I. and Langhelle, G. 1986. Sex and age biased mobility in hawk owls *Surnia ulula*. – *Ornis Scand.* 17: 306–308.

Catling, P. M. 1972. A study of the boreal owl in southern Ontario with particular reference to the irruption of 1968–69. – *Can. Field-Nat.* 86: 223–232.

Cyr, A., Larivée, J. and Dunn, E. H. 1997. Monitoring bird populations with checklist programs. – In: Dunn, E. R., Cadman, M. D. and Falls, J. B. (eds), *Monitoring bird populations: the Canadian experience*. Occas. paper, No. 95, Can. Wildlife Service, pp. 40–42.

Droegge, S., Cyr, A. and Larivée, J. 1998. Checklists: an under-used tool for the inventory and monitoring of plants and animals. – *Conserv. Biol.* 12: 1134–1138.

Duncan, J. R. and Duncan, P. A. 1998. Northern hawk owl. – *Birds N. Am.* 356: 1–27.

Elton, C. and Nicholson, M. 1942. The ten-year cycle in numbers of the lynx in Canada. – *J. Anim. Ecol.* 11: 215–244.

Framstad, E., Stenseth, N. C. and Östbye, E. 1993. Time series analysis of population fluctuations of *Lemmus lemmus*. – In: Stenseth, N. C. and Ims, R. A. (eds), *The biology of lemmings*. Academic Press, pp. 97–115.

Fryxell, J. M., Falls, B., Falls, E. A. et al. 1998. Long-term dynamics of small-mammal populations in Ontario. – *Ecology* 79: 213–225.

Gauthier, J. and Aubry, Y. 1995. Atlas des oiseaux nicheurs du Québec. – Association québécoise des groupes d'ornithologues, Québec.

Génier, A. and Bergeron, J. M. 1996. Impact à court terme de la coupe à blanc avec protection de la régénération sur les petits mammifères en forêt boréale. – Ministère de l'Environnement et de la Faune, Québec.

Gosse, J. W. and Montvecchi, W. A. 2001. Relative abundance of forest birds of prey in western Newfoundland. – *Can. Field-Nat.* 115: 57–63.

Graham, I. M. and Lambin, X. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. – *J. Anim. Ecol.* 71: 946–956.

Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Québec. – *Can. J. Zool.* 54: 2156–2173.

Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – *J. Anim. Ecol.* 60: 353–367.

Hanski, I., Turchin, P., Korpimäki, E. et al. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. – *Nature* 364: 232–235.

Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. – *Oecologia* 67: 394–402.

Hayward, G. D. and Hayward, P. H. 1993. Boreal owl. – *Birds N. Am.* 63: 1–19.

Hayward, G. D., Hayward, P. H. and Graton, E. O. 1993. Ecology of boreal owls in the northern Rocky Mountains, USA. – *Wildl. Monogr.* 124: 1–59.

Hildén, O. and Helo, P. 1981. The great grey owl *Strix nebulosa* – a bird of the northern taiga. – *Ornis Fenn.* 58: 159–166.

- Hipkiss, T. and Ellegren, H. 2002. Sex ratio and age structure of nomadic Tengmalm's owls: a molecular approach. – *J. Avian Biol.* 33: 107–110.
- Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. – *Oecologia* 32: 141–152.
- Johnson, D. R., Swanson, B. J. and Eger, J. L. 2000. Cyclic dynamics of eastern Canadian ermine populations. – *Can. J. Zool.* 78: 835–839.
- Klemola, T., Tanhuanpää, M., Korpimäki, E. et al. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. – *Oikos* 99: 83–94.
- Koenig, W. D. 2001. Synchrony and periodicity of eruptions by boreal birds. – *Condor* 103: 725–735.
- Korpimäki, E. 1985. Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. – *Oikos* 45: 281–284.
- Korpimäki, E. 1986. Gradients in population fluctuations of Tengmalm's owl *Aegolius funereus* in Europe. – *Oecologia* 69: 195–201.
- Korpimäki, E. and Norrdahl, K. 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. – *Oikos* 54: 154–164.
- Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. – *Ecology* 79: 2448–2455.
- Korpimäki, E., Lagerström, M. and Saurola, P. 1987. Field evidence for nomadism in Tengmalm's owl *Aegolius funereus*. – *Ornis Scand.* 18: 1–4.
- Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? – *Oecologia* 88: 552–561.
- Korpimäki, E., Norrdahl, K., Klemola, T. et al. 2002. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. – *Proc. R. Soc. Lond. B* 269: 991–997.
- Korpimäki, E., Klemola, T., Norrdahl, K. et al. 2003. Vole cycles and predation. – *Trends Ecol. Evol.* 18: 494–495.
- Krebs, C. J., Boonstra, R., Boutin, S. et al. 2001. What drives the 10-year cycle of snowshoe hares? – *Bioscience* 51: 25–35.
- Lambin, X. and Graham, I. M. 2003. Testing the specialist predator hypothesis for vole cycles. – *Trends Ecol. Evol.* 18: 493.
- Larivée, J. 2001. Étude des populations d'oiseaux du Québec (EPOQ). Base de données ornithologiques. Rimouski. Association québécoise des groupes d'ornithologues (AQGO).
- Legendre, P. and Legendre, L. 1998. Numerical ecology. – *Develop. Environ. Modelling*, 20. Elsevier.
- Löfgren, O., Hörnfeldt, B. and Carlsson, B. G. 1986. Site tenacity and nomadism in Tengmalm's owl (*Aegolius funereus* (L.)) in relation to cyclic food production. – *Oecologia* 69: 321–326.
- Lundberg, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandia owl species. – *Oecologia* 41: 273–281.
- McLaren, M. A., Thompson, I. D. and Baker, J. A. 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. – *For. Chron.* 74: 241–248.
- Mikkola, H. 1983. Owls of Europe. – Buteo Books, Vermillion S.D.
- Mysterud, I. 1970. Hypotheses concerning characteristics and causes of population movements in Tengmalm's owl (*Aegolius funereus* L.). – *Nytt Mag. Zool.* 18: 49–74.
- Norrdahl, K. and Korpimäki, E. 1995. Effects of predator removal on vertebrate prey populations: birds of prey and small mammals. – *Oecologia* 103: 241–248.
- Norrdahl, K. and Korpimäki, E. 2002. Changes in population structure and reproduction during a 3-yr population cycle of voles. – *Oikos* 96: 331–345.
- Oli, M. K. 2003a. Population cycles of small rodents are caused by specialist predators: or are they? – *Trends Ecol. Evol.* 18: 105–107.
- Oli, M. K. 2003b. Response to Korpimäki et al.: vole cycles and predation. – *Trends Ecol. Evol.* 18: 495–496.
- Pitelka, F. A., Tomich, P. Q. and Treichel, G. W. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. – *Ecol. Monogr.* 25: 85–117.
- Potvin, F., Courtois, R. and Bélanger, L. 1999. Short-term response of wildlife to clear-cutting in Québec boreal forest: multiscale effects and management implications. – *Can. J. For. Res.* 29: 1120–1127.
- Rohner, C., Smith, J. N. M., Stroman, J. et al. 1995. Northern hawk-owls in the nearctic boreal forest: prey selection and population consequences of multiple prey cycles. – *Condor* 97: 208–220.
- Salamolard, M., Butet, A., Leroux, A. et al. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. – *Ecology* 81: 2428–2441.
- Société de la Faune et des Parcs du Québec, Direction du développement de la faune. Atlas des Micromammifères du Québec: base de données [fichier d'ordinateur] Version 2.1, Québec: la Direction, 2000. Base de données réalisée avec le logiciel Microsoft Access 97.
- Sonerud, G. A., Solheim, R. and Prestrud, K. 1988. Dispersal of Tengmalm's owl *Aegolius funereus* in relation to prey availability and nesting success. – *Ornis Scand.* 19: 175–181.
- SPSS Institute Inc. 1999. SPSS 10.0.5, standard version. Chicago, Illinois.
- Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – *Oikos* 87: 427–461.
- Strann, K. B., Yoccoz, N. G. and Ims, R. A. 2002. Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. – *Ecography* 25: 81–87.
- Sundell, J., Huitu, O., Henttonen, H. et al. 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. – *J. Anim. Ecol.* 73: 167–178.
- Swanson, B. J. and Johnson, D. R. 1999. Distinguishing causes of intraspecific synchrony in population dynamics. – *Oikos* 86: 265–274.
- Turchin, P. and Taylor, A. D. 1992. Complex dynamics in ecological time series. – *Ecology* 73: 289–305.
- Turchin, P. and Hanski, I. 1997. An empirical based model for latitudinal gradient in vole population dynamics. – *Am. Nat.* 149: 842–874.
- Turchin, P., Oksanen, L., Ekerholm, P. et al. 2000. Are lemmings prey or predators? – *Nature* 405: 562–565.
- Weber, J. M., Aubry, S., Ferrari, N. et al. 2002. Population changes of different predators during a water vole cycle in a central mountainous habitat. – *Ecography* 25: 95–101.
- Wilson, D. J., Krebs, C. J. and Sinclair, T. 1999. Limitation of collared lemming populations during a population cycle. – *Oikos* 87: 382–398.
- World Resources Institute 2000. Canada's Forests at a Crossroads: an assessment in the Year 2000. – World Resources Institute. Washington, DC.