Effect of cyclic and declining food supply on great grey owls in boreal Sweden

T. Hipkiss, O. Stefansson, and B. Hörnfeldt

Abstract: In this study of 35 years of data, we examine the short-term (cyclic) and long-term relationship between breeding success of great grey owls (*Strix nebulosa* Forster, 1772) and their food supply (bank voles (*Clethrionomys glareolus* (Schreber, 1780)), grey-sided voles (*Clethrionomys rufocanus* (Sundevall, 1846)), and field voles (*Microtus agrestis* (L., 1761))) in northern Sweden. Annual number of owl nests showed a 3 year cyclicity, which as predicted, corresponded to the length of the vole cycle in the region. Mean annual brood size also fluctuated and was positively dependent on the vole supply during the same spring. In this region, there has also been a decline in vole numbers in recent decades, from high-amplitude cycles in the 1970s to subsequent low-amplitude cycles. Correspondingly, and as predicted, mean annual brood size of the owls also declined, although only during the third years of the vole cycle when vole supply in spring and brood size of the owls is at its highest level in high-amplitude cycles. We predict that in the long run the vole decline, associated with increasingly milder winters, and the reduction of the brood size of the owls, especially in years of high owl breeding success, will have serious implications for the population of great grey owls in Scandinavia.

Résumé : L'examen de données sur 35 ans, nous sert à examiner les relations à court (cycliques) et à long termes entre le succès de la reproduction des chouettes lapones (*Strix nebulosa* Forster, 1772) et leur source de nourriture (les campagnols roussâtres (*Clethrionomys glareolus* (Schreber, 1780)), les campagnols gris-roux (*Clethrionomys rufocanus* (Sundevall, 1846)) et les campagnols des champs (*Microtus agrestis* (L., 1761))) dans le nord de la Suède. Il existe un cycle de 3 ans dans le nombre annuel de nids de chouettes, ce qui correspond, comme prédit, à la période du cycle des campagnols de la région. Il y a aussi une fluctuation de la taille des couvées qui est en corrélation positive avec l'approvisionnement en campagnols durant le printemps correspondant. Dans cette région, il y aussi eu un déclin des nombres de campagnols au cours des dernières décennies, depuis les cycles de forte amplitude des années 1970 jusqu'aux cycles subséquents de faible amplitude. Comme prédit, il y a aussi eu un déclin correspondant de la taille annuelle moyenne des couvées des chouettes, mais seulement durant la troisième année des cycles des campagnols, lorsque la présence de campagnols au printemps et la taille des couvées atteignent leur maximum dans les cycles de forte amplitude. Nous prédisons qu'à long terme le déclin des campagnols, associé aux hivers de plus en plus doux, et la diminution de la taille des couvées des chouettes, particulièrement les années de fort succès reproductif des chouettes, vont avoir d'importantes conséquences sur les populations de chouettes lapones en Scandinavie.

[Traduit par la Rédaction]

Introduction

In boreal Fennoscandia, high-amplitude multiannual (3–4 year) cycles of voles have direct effects on the population dynamics of their specialist predators (e.g., Hörnfeldt 1978; Hörnfeldt et al. 1986, 1990, 2005; Korpimäki 1994; Strann et al. 2002). In addition to the multiannual cycles, there has been a long-term decline in vole numbers in boreal Sweden since the early 1980s (Hörnfeldt 1994, 2004, 2008; Hörnfeldt et al. 2005, 2006), and declines with somewhat later timing, but similar characteristics, have also been observed elsewhere in Fennoscandia, as well as in Britain, France, and Hokkaido, Japan (Hanski and Henttonen 1996; Saitoh and Nakatsu 1997; Hansen et al. 1999; Hansson 1999; Henttonen 2000; Bierman et al. 2006; Lambin et al. 2006; Saitoh et al. 2006; Ims et al. 2008). The decline of vole populations is predicted to have far-reaching negative effects on the reproduction and population densities of their predators (Hörnfeldt 1998, 2004; Henttonen 2000; Strann et al. 2002), but so far, this has been little studied. However, the decline of voles in boreal Sweden has clearly been accompanied by a decline in numbers of breeding Tengmalm's owls (*Aegolius funereus* (L., 1758)) and seemingly also in some other specialist predators (Hörnfeldt et al. 2005 and references therein).

The great grey owl (*Strix nebulosa* Forster, 1772) is a large nocturnal raptor of the boreal coniferous belt (Mikkola 1983; König et al. 1999). It breeds mainly in extensive, older coniferous forests (Sulkava and Huhtala 1997; König et al. 1999), nesting on tree stumps, in the abandoned nests of other raptors (Mikkola 1983; Sulkava and Huhtala 1997), and man-made nest platforms (Bull et al. 1987; Stefansson 1997). In Sweden the great grey owl is distributed throughout the boreal zone, but is most frequently found in the northeasternmost parts of the country (Stefansson 2007).

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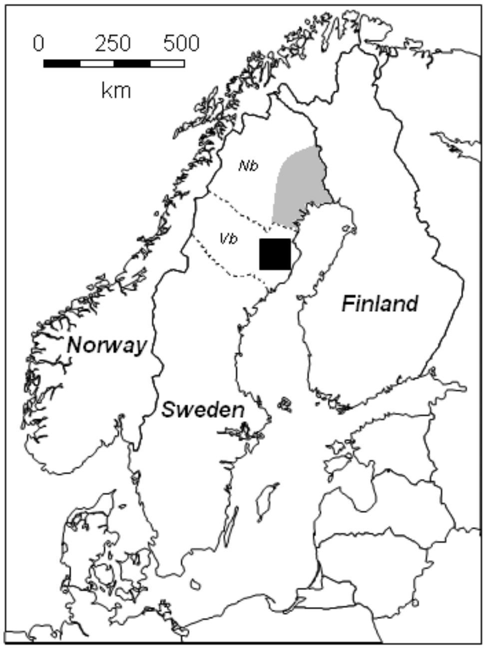
Modern forestry activity is regarded to have had a negative effect on the owl's breeding habitat and is considered the main threat to the species in Sweden (Stefansson 1997, 2007), but on the other hand may have provided more open hunting habitat (Sulkava and Huhtala 1997). The great grey owl feeds mainly on voles (Mikkola 1983 and references therein; Sulkava and Huhtala 1997), and numbers of nests differ greatly between good and bad vole years (Mikkola 1983). The great grey owl is irruptive (Hildén and Helo 1981; Mikkola 1983; Stefansson 1997; König et al. 1999) and considered nomadic, leaving areas where the food supply runs out and settling to breed in areas where they find food, although nomadic breeding behaviour has yet to be fully confirmed from ringing recovery data (cf. Hildén and Helo 1981; Mikkola 1983).

We are not aware of any published quantitative long-term studies of the great grey owl and its prey, so the relationship between food supply and breeding success has generally been inferred rather than measured. If a close relationship between great grey owls and their vole prey is found, as we hypothesize, we predict that the recent decline in vole numbers in boreal Sweden has had negative consequences on the owls' breeding success. The purpose of this study is thus twofold: to test the hypothesis that there is a cyclic relationship between populations of great grey owls and voles in northern Sweden, and to test the prediction that a recent decline in voles in the region has had a negative effect on the owls' breeding success.

Fig. 1. Nests of great grey owl (*Strix nebulosa*) were located in the shaded area, while voles (bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*)) were trapped in the 100 km × 100 km area marked by the solid square. Broken lines mark the boundaries of the northernmost Swedish counties of Norrbotten (*Nb*) and Västerbotten (*Vb*).



Materials and methods

Owl monitoring

In the 1970s and 1980s, suitable forest habitat in Norrbotten county, northern Sweden, was surveyed for breeding sites of great grey owls (Stefansson 1997; Fig. 1). This area forms part of the owl's stronghold in Sweden (Stefansson 2007). Known nests of great grey owls from the 1970s until the present day were visited in late April to mid-May to check whether they were occupied. Occupied nests were revisited at the same brooding stage throughout the study period when the young were half-grown, i.e., approximately 3–4 weeks old, to obtain a measure of the brood size (Stefansson 1997). The young were ringed where the nest and young were accessible. The number of nests checked each year varied slightly, since during some years more remote nests were inaccessible, and throughout the study period new nests were occasionally discovered, while others were lost. Nest platforms were erected and maintained at many sites to replace natural nests that were lost owing to forestry operations or natural causes. In this study, we limit our analyses of number of nests per year to an investigation of short-term (cyclic) variation within the time series, but cannot accurately describe, and thus refrain from firm conclusions on, any long-term trends throughout the time series. For brood size, however, we analyse both short-term and long-term variations.

Vole monitoring

Indices of natural food supply for the owls were obtained from a running survey (now part of the Swedish Environmental Protection Agency's National Environmental Monitoring Programme) of small mammals, in which snap-trapping has been carried out twice yearly since autumn 1971 (Hörnfeldt 2008). Sampling was carried out for three consecutive nights in spring (late May) and autumn (late September) in 58 regularly distributed 1 ha plots in a 100 km × 100 km area in Västerbotten county, northern Sweden (Fig. 1; for more details see Hörnfeldt 1978, 1994, 2004). The pooled number of voles (bank voles (*Clethrionomys glareolus* (Schreber, 1780)), grey-sided voles (*Clethrionomys rufocanus* (Sundevall, 1846)), and field voles (*Microtus agrestis* (L., 1761))) trapped per 100 trap-nights was used as an index of food supply in spring and autumn. We used the time-series data of voles from Västerbotten as a proxy for the food situation for the great grey owl in Norrbotten, since no vole monitoring has been carried out there. Since numbers of nests of Tengmalm's owl, another highly dependent specialist predator on voles (Mikkola 1983; Hörnfeldt et al. 1990), in Västerbotten during 1980–2003 (data from Hörnfeldt et al. 2005) was highly correlated with the number of nests of great grey owls in the same years (cross-correlation function: $r = 0.70$, $p < 0.05$), it suggested that the vole data from Västerbotten can be used as an acceptable proxy for the vole supply in Norrbotten. The years of the study were categorized according to the phases of the 3- to 4-year vole cycle. We classified the phase according to rate of change in numbers of voles during the reproductive season in summer, i.e., from spring to autumn. The transition between successive cycles is characterized by a major shift in this rate of change from low values at the end of the previous cycle to high values at the beginning of the next cycle (Hörnfeldt 1994, 2004). Thus, this first year of

Fig. 2. (*a*) Number of nests of great grey owls (*Strix nebulosa*) located in Norrbotten, Sweden, during the springs of 1973–2007 and pooled density indices of voles (bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*)) in Västerbotten, Sweden, expressed as the number of voles trapped per 100 trap-nights during (*b*) the springs of 1972–2007 and (*c*) the autumns of 1971–2007.

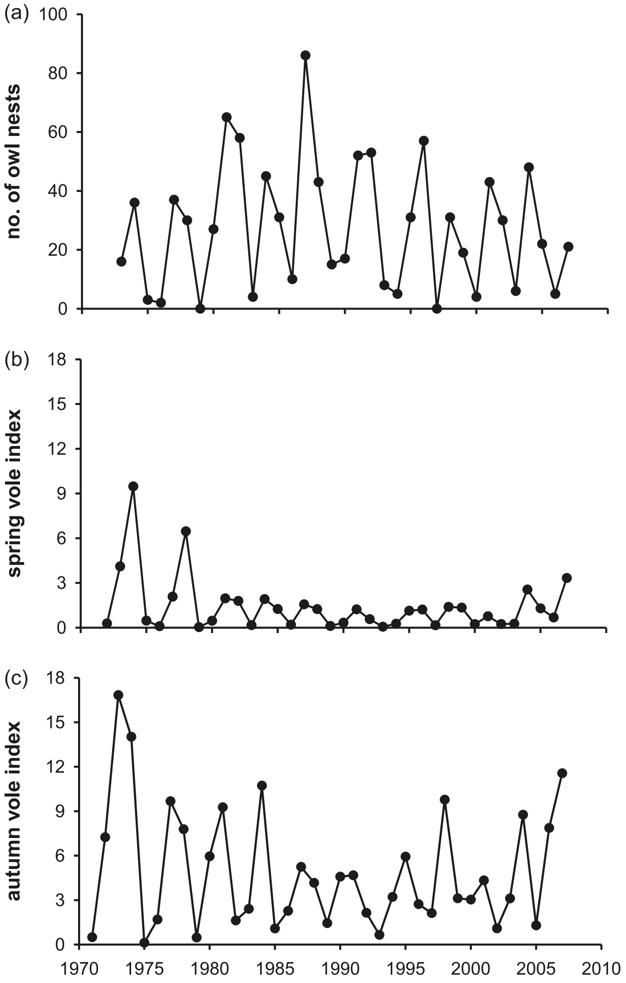
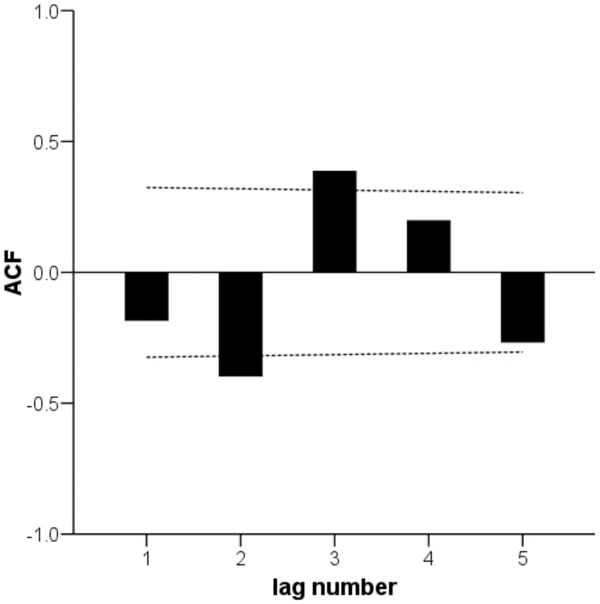


Fig. 3. Autocorrelation function (ACF) for number of nests of great grey owls (*Strix nebulosa*) in Norrbotten, Sweden, during the springs of 1973–2007. The broken lines represent 95% confidence intervals.



the cycle represents phase 1 (or the increase phase), and is often characterized by very low vole numbers in spring at the time of the owls' breeding. The subsequent years represent phases 2 and 3 (and in some cycles phase 4). The classification was a common judgement based on *C. glareolus* and *M. agrestis* throughout and on *C. rufocanus* up to 1989, after which judgements based on this species were considered less reliable because of the very heavy decline and low numbers in this species (cf. Hörnfeldt 2004). In the increase phase, at least two of the vole species showed the major shift in rate of change in numbers.

Data analysis

Autocorrelation function (ACF) was used to analyse the short-term periodicity of annual fluctuations of numbers of nests of great grey owls in Norrbotten. This variable was natural-log-transformed prior to time-series analysis, after first adding a constant of one because of the presence of zeros in the time series (2 years with no nests). Cross-correlation function (CCF) was used to analyse the covariance between numbers of owl nests (transformed as above) and the spring and autumn vole indices. Weighted least squares linear regression was used to analyse the relationship between mean annual brood size and food supply in the current spring, current autumn, and previous autumn. Mean annual brood size was weighted according to the number of broods found that year. This accounts for the difference in the number of broods that make up each year's annual mean, and prevents potential outlying brood sizes in years when the sample size was very low from excerting a disproportionate influence on the results. The validity of the model was checked by visually examining the raw residuals. The long-term trend in annual brood size was investigated using three separate linear regression models for years categorized as the subsequent phases (years) 1, 2, and 3 of the vole cycle. All statistical analyses were carried out using SPSS version 15.0 (SPSS Inc., Chicago, Illinois).

Results

The number of nests of great grey owls fluctuated greatly among years, ranging from zero nests (in 1979 and 1997) to 86 (in 1987) (Fig. 2*a*). Autocorrelation function indicated a 3 year cyclicity, since lag-3 showed a significant positive correlation ($r = 0.37$, $p < 0.05$; Fig. 3), roughly corresponding to the period length of the cycles of voles in the region. Cross-correlation function showed that the number of nests per year covaried with the vole index during the same spring ($r = 0.71$, $p < 0.05$), but not the previous autumn ($r = 0.28$, $p > 0.05$). Weighted least squares regression analysis showed that mean annual brood size was significantly positively dependent on the supply of voles in spring, but not in the current or previous autumn (Table 1; Fig. 4). Thus, mean annual brood size varied greatly among years, reflecting

Fig. 4. Mean annual brood size (no. of nestlings) of great grey owls (*Strix nebulosa*) in Norrbotten, Sweden, during the springs of 1973–2007 against spring vole (bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*)) index (no. of voles trapped per 100 trap-nights). R^2 value of quadratic best fit line is 0.68.

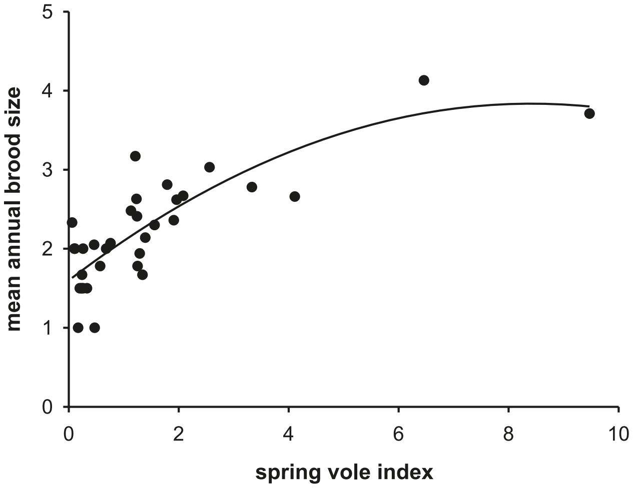


Table 1. Results of weighted least squares regression of the effects of vole (bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*)) supply in the current spring, current autumn, and previous autumn on mean annual brood size of great grey owls (*Strix nebulosa*) during the springs 1973–2007 (*N* = 35 years).

Vole index	*β*	*t*	*p*
Previous autumn	–0.24	–1.13	0.27
Current spring	0.98	3.61	0.01
Current autumn	–0.19	–0.90	0.37

Note: The *β* values are standardized. Annual brood-size values were weighted according to the total number of broods that year. R^2 (adjusted) value of the significant model (voles in current spring) is 0.49.

Fig. 5. Mean annual brood size (no. of nestlings) of great grey owls (*Strix nebulosa*) in Norrbotten, Sweden, during the springs 1973–2007. Note that no broods were found in 1979 and 1997. Open circles represent phase (year) 1 of the vole cycle; shaded circles represent phase 2; solid circles respresent phase 3; solid squares represent phase 4.

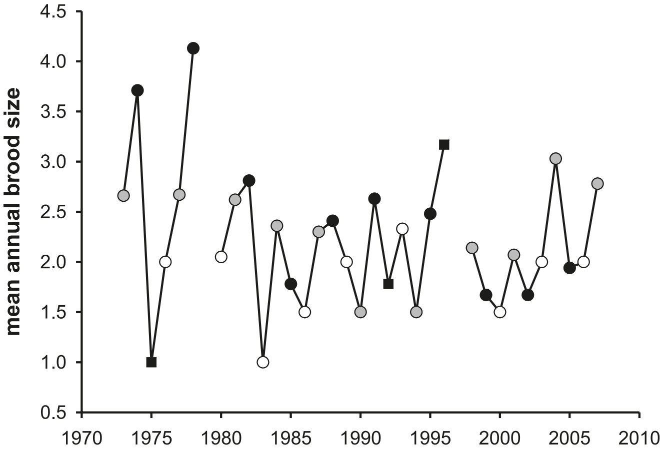


Table 2. Results of weighted least squares regression analyses of mean annual brood size of great grey owls (*Strix nebulosa*) against phase (year) of the vole (bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*)) cycle.

	n	*β*	*t*	*p*
Phase 1	9	–0.19	–0.52	0.62
Phase 2	11	0.06	0.20	0.85
Phase 3	10	–0.76	–3.30	0.01

Note: Three separate analyses were carried out for phases 1, 2, and 3 of the vole cycle. The *β* is standardized. Annual brood-size values were weighted according to the total number of broods that year. R^2 (adjusted) value of the significant model (phase 3) is 0.52.

fluctuating vole numbers (Fig. 5). A long-term decline during the 35 year time series in mean annual brood size is only apparent when the annual results are separated according to vole phase. Mean annual brood size declined only during phase 3 of the vole cycle (Table 2). During this phase, vole numbers in spring (Fig. 2*b*) and owl brood size (Fig. 5) represented the cyclic peaks and were at very high levels in the 1970s before the heavy vole decline. In contrast, during the last 10 years, phase 3 showed very low brood sizes that were consistently lower than in phase 2.

Discussion

Our results quantitatively demonstrate for the first time the cyclic relationship between vole supply and the number of nests and brood size of great grey owls in northern Sweden. Mean annual brood size was positively correlated with the vole supply in spring, a relationship also found in Tengmalm's owls (Hörnfeldt et al. 1990). While the number of breeding great grey owls has been reported to vary greatly between years (Mikkola 1983; Stefansson 1997), and was hypothesized to show short-term cycles varying with vole supply, this is the first time a cyclic relationship between vole numbers and owl breeding success has been shown. The more or less synchronous fluctuations of nests of great grey owls with vole supply may be partly explained by immigration of nomadic individuals (cf. Introduction). However, the type of data presented here cannot discriminate between this or whether variable proportions of stationary individuals respond and breed in relation to the prevailing food supply.

As predicted, we observed an effect of the recent regional decline in vole numbers on the breeding success of great grey owls. Interestingly, this was only noticable during the third year of the vole cycle. The decline in vole density in northern Sweden from high-amplitude cycles in the 1970s to the subsequent low-amplitude cycles is characterized by an increased frequency and severity of winter declines, leading to lower spring densities especially during the third years of the cycles (Hörnfeldt 2004). This decline is also reflected in a decrease in breeding density of Tengmalm's owls in the region, from high-amplitude cycles in the early

1980s to low-amplitude cycles afterwards that seemed to fade out in the early 2000s (Hörnfeldt et al. 2005). We do not consider our data on numbers nests of great grey owls to be robust enough to elucidate any long-term trends. Any consistent decline during the time series (Fig. 2) may be masked, at least in the earlier years of the study, by increasing knowledge of potential nest sites with time. However, we predict that the long-term decline in brood size during the third phase of the vole cycle, when vole numbers in spring and owl brood size are at their highest levels during "normal" high-amplitude vole cycles like those in the 1970s, will eventually also lead to a decline in owl population size. To monitor this it is necessary to adopt a more accurate measurement of the size of the breeding population and the extent of nomadism; the population of great grey owls in northern Sweden may be supported by immigration from areas where voles still display high-amplitude cycles.

If any other available long-term data sets on brood-size variation for other specialist vole or lemming predators are analysed, we predict that long-term declines are most likely to be found late in the cycles in analogy with our findings for the great grey owl. According to publications, long-term contemporary data sets on population size or breeding performance of vole specialist predators on the one hand and their staple food supply on the other hand seem to be rare. Few attempts have been reported that link the recent long-term decline of vole populations to the fate of the predator populations. In addition to our findings here for the brood size of the great grey owl and previously for numbers of breeding Tengmalm's owls (Hörnfeldt et al. 2005), we know of few other long-term studies where a decline in both predator numbers or breeding success and their prey have been monitored. Numbers of territories of Tengmalm's owls and long-eared owls (*Asio otus* (L., 1758)) declined in coastal areas in southern Finland from the 1980s and onwards, probably as a result of declining vole populations (Solonen 2004), although the vole data seemed insufficient for a definitive conclusion. Similarily, the arctic fox (*Alopex lagopus* (L., 1758)) has declined since the mid-1980s in the Scandinavian mountains (Angerbjörn et al. 1995), and numbers of migrating hen harriers (*Circus cyaneus* (L., 1766)) and rough-legged buzzards (*Buteo lagopus* (Pontoppidan, 1763)) at Falsterbo, southern Sweden, in autumn have decreased during recent decades (Kjellén and Roos 2000). However, in both these latter studies, where declines in predator numbers were ascribed to decreasing small-mammal numbers, this was not supported by quantitative estimates of rodent abundance.

The long-term decline in vole numbers and change in their dynamics in northern Fennoscandia is thought to be related to increasingly mild and wet winters in the region (Hörnfeldt 2004; Solonen 2004; Hörnfeldt et al. 2005; Bierman et al. 2006; Ims et al. 2008). During milder winters, with fluctuating periods of thaw and freezing, shortening of the snow period and ice-bark formation on the ground denies voles and lemmings their subniveal refuge from predators and adverse weather, decreasing their survival and leading to large winter declines (Aars and Ims 2002; Hörnfeldt 2004; Solonen 2004). Predicted increases in temperature associated with global warming seem likely to exacerbate the so-called collapse of high-amplitude vole cycles and lead to lower numbers of their specialist predators (Hörnfeldt 1998, 2004; Strann et al. 2002; Solonen 2004; Hörnfeldt et al. 2005; Ims et al. 2008). The great grey owl is red-listed (as near-threatened) in Sweden (Stefansson 2007), so a prolonged period of low supply or a further decrease in its most important food supply in spring threatens the Scandinavian population in the long-term and is therefore an important conservation issue.

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