1 Introduction

Vertebrate predators, particularly large charismatic apex predators, have traditionally elicited much esteem and deference, because they have been depicted as being beautiful, majestic and strong. Predator–prey interactions are also an intriguing topic in ecology and evolution. Most people would be impressed by the skilful hovering of Eurasian kestrels in the sky, which then swoop down towards a vole hidden in the undergrowth, or by the auditory location of voles by the great grey owl (*Strix nebulosa*) underneath a 60-cm-deep layer of compacted snow, through which the owl dives and often successfully captures the voles. It is also intriguing that snowy owls '*Bubo scandiaca*' in the northern tundra are able to track peak densities of lemmings thousands of kilometres apart, and find and settle in areas with high lemming densities to rear broods of ten owlets. Territories of birds of prey, particularly the large top avian predators such as golden eagles and eagle owls, are expected to have a high biodiversity value (Sergio et al. 2005, 2006), which suggests that conservation efforts focusing on avian predators can be ecologically justified.

This book is intended for general readers interested in nature, and in particular for ecology students, professional ecologists, and other scientists who are interested in life-history evolution, parental care and mating systems, population dynamics and predator–prey relationships of vertebrate animals. In addition, we expect that bird-watchers, naturalists, gamekeepers, and farmers, as well as forest managers, would also be interested in this book, so we will attempt to write in a style that is easily readable both for members of the public and for professionals and scholars. Many keen bird-watchers in temperate areas are making increased efforts to watch northern species, and are particularly interested in birds of prey. At present, there are not many relevant books available, because most books about avian predators are concerned with species that mainly live in temperate areas, or have a community-wide approach and cannot therefore concentrate on individual predator species in great detail. The overriding interest of farmers and forest managers might be based on the fact that owls are widely considered as biological agents controlling small mammal densities. In the peak phase of the population cycle, voles can cause serious damage to forestry and agriculture, and the annual cost can run into many millions of euros, as in Finland (Huitu et al. 2009).

Most books on the ecology and behaviour of birds and other organisms deal with species that live in temperate, subtropical and tropical regions with no marked between-year fluctuations in main environmental characteristics. In the Eurasian and North American boreal and arctic areas, there are marked between-year cyclic population fluctuations of many animal species, including some insects, voles, lemmings, shrews

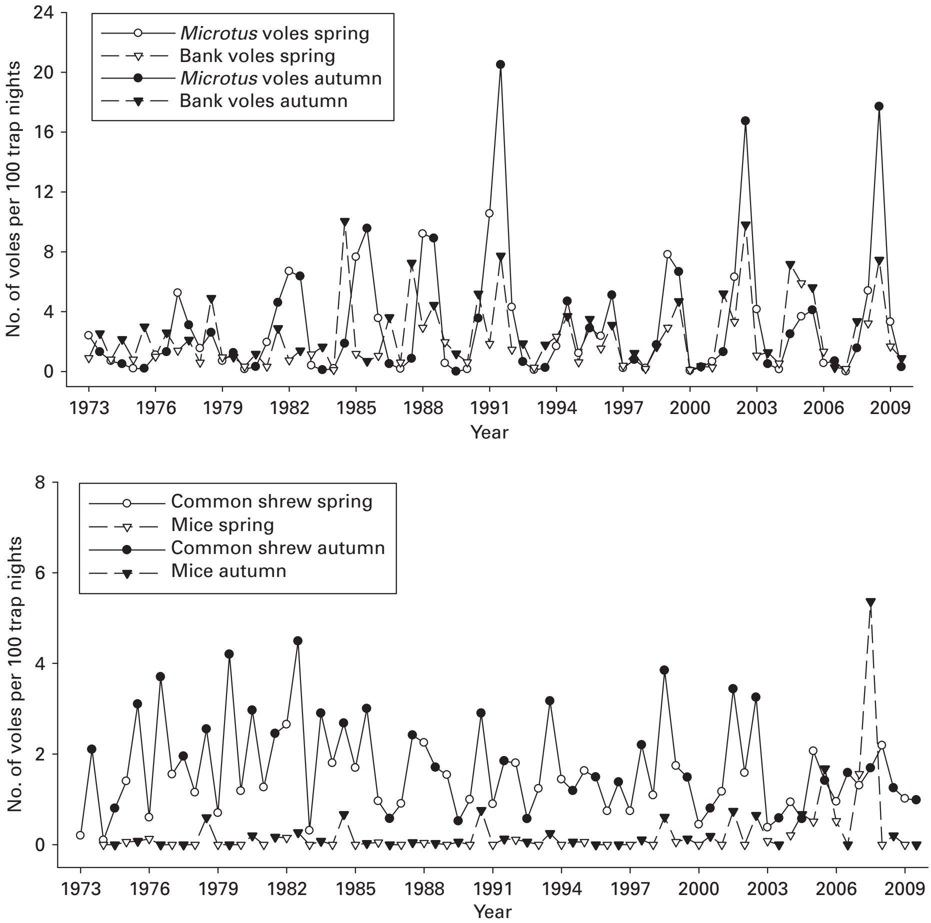

Fig. 1.1. Abundance estimates (no. of individuals snap-trapped per 100 trap-nights) of *Microtus* voles (circles) and bank voles (triangles) (upper panel), and common shrews (circles) and pooled harvest and house mice (triangles) (lower panel, note different scale of *y*-axis) in the Kauhava region, western Finland in spring (May; open symbols) and autumn (September; closed symbols) during 1973–2009 (Korpimäki et al. 2002, 2005a and unpublished data).

and small game animals (e.g. hare and forest grouse), and their avian and mammalian predators. Of these, the most regular cyclic fluctuations have been found in small rodents in Eurasia and in snow-shoe hares in North America, and in their avian and mammalian predators in both continents (Boutin et al. 1995, Korpimäki and Krebs 1996, Klemola et al. 2002, Korpimäki et al. 2004). These multi-annual cyclic fluctuations have fascinated ecologists, naturalists and local people living in these areas for a long time (e.g. Collett 1878, Collin 1886, Elton 1942, Elton and Nicholson 1942, Hagen 1952, Siivonen 1954, 1957). Although some researchers have recently claimed that these regular high-amplitude population cycles of small mammals and their predators in northern areas have faded out (Hörnfeldt et al. 2005, Ims et al. 2008), possibly because of climate change, long-term data from our study area (Fig. 1.1; Korpimäki et al. 2005a, 2008) and elsewhere in northern Europe (Aunapuu and Oksanen T. 2003, Oksanen T. et al. 2008, Brommer et al. 2010, Lehikoinen et al. 2011) show that the heart of the well-known and fascinating north European vole and owl cycle is still beating.

The densities of most vole populations in central and western Europe fluctuate only seasonally and thus exhibit low densities in spring and higher densities in autumn, after the reproductive season of voles (see Hansson and Henttonen 1988). In addition, there are also some local multi-annual low-amplitude cyclic fluctuations of voles of the genus *Microtus* and their avian predators in central and western Europe (figure 14.1 in Taylor I. 1994, Lambin et al. 2000, Salamolard et al. 2000, Tkadlec and Stenseth 2001). However, there are also at least five distinct differences in the population dynamics of voles between west-central Europe and northern Europe.

1. The northern multi-annual vole cycles cover hundreds of thousands of square kilometres in pristine boreal and arctic ecosystems and in human-made forest plantations and agricultural fields (Kalela 1962), whereas the 3-year population cycle of, for example, field voles *Microtus agrestis* in Kielder Forest, Northumberland, England, is a smaller-scale phenomenon covering approximately 600 km^2 in man-made forest plantations (Lambin et al. 2000).
2. The low phases of northern vole cycles reach densities 1 to 2 orders of magnitude lower than in temperate Europe (for example, <1 per hectare in northern Europe vs. 25–50 per hectare in Kielder Forest) (Henttonen et al. 1987, Oksanen T. et al. 1999, Lambin et al. 2000).
3. Northern vole cycles are high-amplitude fluctuations, characterised by 50- to 500-fold (sometimes up to 1000-fold) differences between peak and minimum densities (Hanski et al. 1991, Oksanen L. and Oksanen T. 1992), whereas in temperate Europe differences between peaks and lows are only about 10-fold (Lambin et al. 2000).
4. The cycles of Kielder Forest are spatially synchronous at a small scale only (8–20 km; Lambin et al. 1998), whereas the northern vole cycles are synchronous at an essentially larger spatial scale (70–600 km; Henttonen et al. 1987, Hanski et al. 1991, Huitu et al. 2003b, Sundell et al. 2004).
5. In northern Europe, populations of field voles fluctuate in close temporal synchrony with those of other herbivorous voles of the genera *Microtus* and *Myodes* (earlier *Clethrionomys*) species, and even with insectivorous shrews (*Sorex* spp.) (Fig. 1.1). All of them show their lowest population densities simultaneously (Henttonen et al. 1987, 1989, Hanski and Henttonen 1996), whereas interspecific synchrony with the aforementioned species or other small mammals has not been documented in temperate Europe.

These five differences in population dynamics between temperate and northern Europe indicate clear differences in the underlying mechanisms. In particular, these five characteristics are also crucial for the predators that subsist on voles as their main foods.

This book tells the story of the boreal owl (*Aegolius funereus* L.; Tengmalm's owl in Europe): its hunting modes, habitats and foods, its interactions with prey, parental care and mating systems, reproduction, dispersal, survival and mortality, family planning, population regulation and conservation in boreal forests. The boreal owl used to be the most numerous predatory bird in Eurasian boreal coniferous forests, and it is also widespread in North American coniferous forest regions including the Rocky Mountains. Here we use the American English species name, the boreal owl, rather than the British English species name, Tengmalm's owl, which originates from the Swedish physician and naturalist, Peter Gustaf Tengmalm (1754–1803). P. G. Tengmalm was interested in owls and improved upon Linnaeus' owl classification in a paper submitted to the Swedish Academy of Sciences. Johann Friedrich Gmelin named an owl after him (*Strix tengmalmi*) in 1788, but believed mistakenly that P. G. Tengmalm had been the first to describe this species for science. We think that 'boreal owl' describes this species better than 'Tengmalm's owl', because this owl species occupies boreal (taiga) forests in Eurasia and North America. In addition, at least in the Finnish language, human names are not normally used as the names of animal species.

Boreal owls subsist on small mammals (voles, mice, lemmings and shrews), most of which show cyclic population fluctuations in Eurasian boreal areas with a cycle length of 3–4 years (see Fig. 1.1 for an example of a 3-year vole cycle in western Finland). In the course of the 3–4-year cycle, vole populations show 50- to 250-fold fluctuations in their densities. Therefore, vole-eating predators such as boreal owls may experience 'lean' periods of 1–2 years in length and 'fat' periods of 1–2 years in length during a single vole cycle. These owls need to adjust their main behavioural and life-history traits to these cyclically varying 'fat' and 'lean' periods. They should be able to survive 'lean' periods either by long-distance dispersal movements, because vole cycles are synchronous over large areas (see above), and/or by shifting to alternative prey, such as small birds, because the densities of all main small mammal populations are synchronously low in northern areas. On the other hand, owls should also be able to adjust their reproductive effort so that they can take full advantage of an abundance of food, for example by producing large clutches and broods with high-quality offspring during 'fat' periods. Our own long-term studies (>40 years) and studies by our colleagues elsewhere in Europe and in North America show that boreal owls are the avian predators that are apparently best adapted to these cyclically varying environmental conditions. In addition, they have to cope with seasonally varying environmental conditions, because the distribution of these owls covers regions where long snowy winters are, or at least have been, regular and predictable. In boreal regions, long-lasting deep snow cover protects small mammals against aerial predators, and boreal owls are too small to penetrate a deep snow layer and to catch voles hiding beneath the snow.

The main purposes of our book are first to give a short introduction to the species, and then to describe and discuss the complex interactions of boreal owls with their main prey species. Next, we aim to examine the behavioural and life-history (demographic) adaptations of boreal owls to environmental conditions that markedly fluctuate both seasonally and multi-annually, cyclically in a predictable manner, in boreal forests. We investigate whether boreal owls are able to time their reproductive effort so as to maximise reproductive success; in other words to 'plan' their families. Fourth, we explore the factors that might regulate boreal owl populations. Fifth, we aim to reveal the possible detrimental effects of loss of boreal coniferous forests due to modern forestry practices on boreal owl populations. Finally, we intend to explore how boreal owl populations could be managed in order to sustain viable populations.

Cambridge University Press
978-0-521-11371-7 - The Boreal Owl: Ecology, Behaviour and Conservation of a Forest-Dwelling Predator
Erkki Korpimäki and Harri Hakkarainen
Excerpt
More information

2 The boreal (or Tengmalm's) owl: in brief

Source: Drawn by Marke Raatikainen

2.1. Plumage and morphological characteristics

The boreal owl is a quite small fieldfare-sized long-winged avian predator in Eurasian and North American coniferous (taiga) forests. This almost entirely night-active (nocturnal) owl is very inconspicuous in the daytime but is sometimes seen perched on a branch of a dense conifer, usually a spruce tree. It stands motionless in an upright position near the trunk in the manner of a long-eared owl. Therefore, humans are not often able to observe boreal owls, but their loud primary song, 'pu' or 'po', has been heard by many people who live and work in the countryside (see Chapter 2.3). A long time ago, laymen and hunters in the Finnish countryside believed that this vocalisation was made by the arctic hare *Lepus timidus*. In the boreal owl, the sexes are alike but females are substantially larger than males.

In comparison to the similar-sized little owl, *Athene noctua*, boreal owls have a disproportionately large head, longer wings and a very distinct facial disc. The greyish-white facial disc is framed by a brown-black border and highlighted by raised white eyebrows, which give the owl a surprised expression (Fig. 2.1). This expression is

Fig. 2.1. The greyish-white facial disc of the boreal owl is framed by a brown-black border and highlighted by raised white eyebrows. The upper part is dark brown with white spotting, and the under-part is creamy white, broadly streaked with dark brown or russet. Photo: Pertti Malinen. (For colour version, see colour plate.)

Fig. 2.2. Fledglings of boreal owls are dark brown with very distinct white 'eyebrow' markings and some white spots on the scapulars and wing coverts. Photo: Benjam Pöntinen. (For colour version, see colour plate.)

complemented by the large bright yellow-black eyes. The upper part of the plumage is dark brown with white spotting, which gives the species its Finnish name '*helmipöllö*' and its Swedish name '*pärluggla*' ('pearl owl'). The under-part is creamy white, broadly streaked with dark brown or russet. This streaking is especially dense on the breast but less so on the lower belly. Between-individual colour variation in adult owls is substantial: some are more greyish, whereas others have a more reddish-brown (russet) colour on their upper parts. Yearling owls are probably darker than older owls. The short tail is brown above, with narrow white cross-bars. As in most other northern owl species, the legs and feet are densely covered with white-grey feathers, which is also a striking difference from little owls. The claws are blackish-brown and the bill is wax-yellow. The closest allospecific, the saw-whet owl *Aegolius acadicus*, is smaller than the boreal owl, has chestnut rather than greyish-brown streaking on the breast, and the general tone of its upper part is reddish-brown rather than greyish-brown.

The coloration of young boreal owls during the late nestling, fledging and post-fledging periods differs distinctly from that of adults. Young owls are dark brown overall, even darker and sootier on the facial disc, with very distinct white 'eyebrow' markings (Fig. 2.2). They have some white spots on the scapulars and wing coverts. Young saw-whet owls have a paler two-tone breast and belly than young boreal owls.

2.2. Moulting, ageing and sexing

Some European owls moult all their primary feathers each year, whereas boreal owls take more than a year to replace the primaries of the juvenile plumage (Altmüller and

Fig. 2.3. The wings of yearling (2nd calendar year) boreal owls have only dark brown and unworn primary and secondary feathers. Photo: Rauno Varjonen. (For colour version, see colour plate.)

Kondrazki 1976, Glutz von Blotzheim and Bauer 1980). In the post-juvenile moult during the post-fledging and first independence periods of the young, boreal owls moult their first adult plumage, including all the primary and secondary feathers of the wings. Therefore, in their first breeding season at the age of 1 year (i.e. as yearlings), parent boreal owls have only one age class of primary and secondary feathers, which are dark brown and unworn (Fig. 2.3). From late June–July up to September of the second calendar year of their life, the owls moult between one and six (on average four) outermost primaries. Therefore, in their second autumn and breeding season the next spring, 2-year-old owls have two age classes of primaries on their wings: the outermost dark-brown unworn 1–6 primary feathers and the light-brown worn innermost 4–9 primaries (Fig. 2.4). In the third calendar year of life, the owls moult a middle group of their primaries, usually 2–4 primaries. Therefore, 3-year-old owls have three age classes of primaries on their wings (Fig. 2.5). At the age of 4 years, the wave of primary moulting proceeds towards the innermost primaries; the ninth and tenth innermost primaries are first moulted only at the age of 5 years (Fig. 2.6).

To age non-ringed boreal owls trapped at the nest or outside the breeding season, this moult pattern method has been tested by using known ages of ringed individuals in German (Schwerdtfeger 1984, 1991), Finnish (Korpimäki and Hongell 1986, Lagerström and Korpimäki 1988) and Swedish (Hörnfeldt et al. 1988) populations. It has been found that it is reasonable to age the owls into at least three age classes: 1-year, 2-year and +2-year-old individuals. Hörnfeldt et al. (1988) concluded that 90% of females and >80% of males can also be aged as 3-year-old individuals. They also gave detailed descriptions of the duration and patterns of moult of boreal owls (see also Erkinaro 1975, Glutz von Blotzheim and Bauer 1980). All in all, this age determination method has proved to be very valuable in individual-level population studies of boreal owls, because most unknown-age adult owls can be reliably aged into these three age

Fig. 2.4. Two-year-old (3rd calendar year) boreal owls have the outermost dark-brown unworn 1–6 (in this case 5) primary feathers and the light-brown worn innermost 4–9 (in this case 5) primaries. Photo: Rauno Varjonen. (For colour version, see colour plate.)

Fig. 2.5. Three-year-old (4th calendar year) boreal owls have three age classes of primaries on their wings. This male has moulted the fourth to sixth primary feathers in the previous autumn, the first three primaries in the autumn before that, and the four innermost primaries are still unmoulted. Photo: Rauno Varjonen. (For colour version, see colour plate.)

classes when trapped and ringed for the first time. Nestlings can be reliably aged by measuring wing length (Fig. 2.7): the accuracy of age estimation appears to be 1 day up to the age of 3 weeks, and thereafter it is 2 days up to the age of 4–5 weeks. The body mass is apparently a reliable estimate of age of the young only up to the age of 2 weeks (Fig. 2.8), because the body mass of nestlings and fledglings varies in relation to main food

Fig. 2.6. At the age of 4 years, the wave of primary moulting proceeds towards the innermost primaries; the 9th and 10th innermost primaries are first moulted only at the age of 5 or more years. This >7-year-old male has not yet moulted the 10th innermost primary. Photo: Rauno Varjonen. (For colour version, see colour plate.)

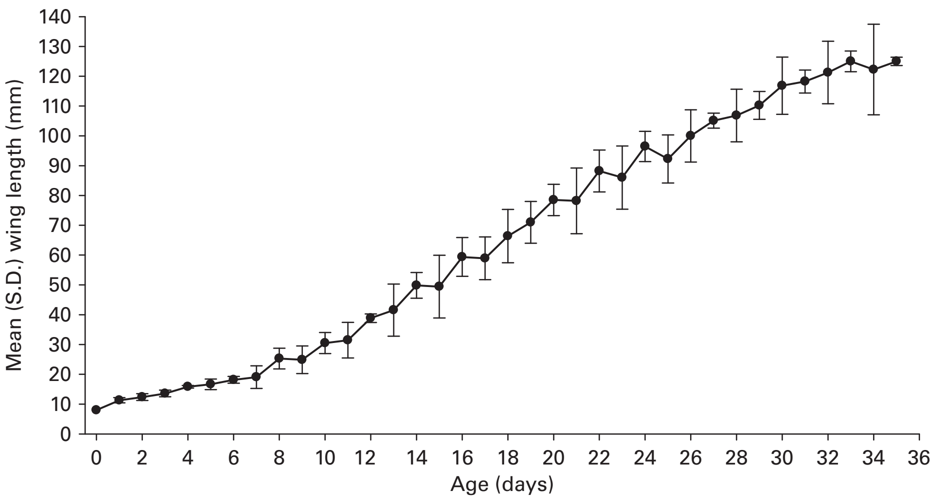

Fig. 2.7. Mean (s.d.) wing length (mm) of boreal owl chicks from hatching to the age of 35 days. Pooled data from chicks from nine nests during 1974–5, 1977–9 and 1980 (Korpimäki 1981 and unpublished data).

abundance, and there is also hatching-order and intersexual variation in body mass (Kuhk 1969, 1970, Korpimäki 1981, Carlsson B.-G. and Hörnfeldt 1994, Schwerdtfeger 2000, Valkama et al. 2002, Suopajärvi P. and Suopajärvi M. 2003).

Sexing of breeding owls is easy, because females, but not males, have very distinct brood patch; only females incubate eggs and brood the young (Korpimäki 1981, Mikkola