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Authors: Korpimäki, Erkki, Hakkarainen, Harri, Laaksonen, Toni, and Vasko, Ville

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Responses of owls and Eurasian Kestrels to spatio-temporal variation of their main prey

Erkki Korpimäki¹, Harri Hakkarainen¹, Toni Laaksonen¹ & Ville Vasko¹

¹Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland (ekorpi@utu.fi)

Many owl species and also Eurasian Kestrels *Falco tinnunculus* (hereafter Kestrels) feed mainly on voles of the genera *Microtus* and *Clethrionomys* in North Europe. Three-to-four-year population cycles of voles are characteristic in boreal and arctic areas of North Europe. These multi-annual population cycles of voles are different from those in temperate areas of Europe, because the amplitude of the cycles is much higher (50–200-fold), the spatial synchrony extends over 80–600 km, and there are steep summer declines of voles in the north (Korpimäki *et al.* 2004, 2005b). In addition, population densities of herbivorous voles and mice, and even of insectivorous shrews fluctuate in close synchrony (Korpimäki *et al.* 2005a).

The three-year population cycle of voles has been prevailing in western Finland during >30 years. In the low phase of the cycle, vole densities are low during the breeding season of owls and Kestrels but slowly start to recover in late summer. In the increase phase of the cycle, vole densities are intermediate during the egg-laying period of owls and Kestrels but fastly increase in the course of the summer. In the decline phase of the cycle, vole densities are still intermediate in early spring but decline to low numbers at the end of nestling and fledging periods of owls and Kestrels (Fig. 1 in Korpimäki & Hakkarainen 1991). These cyclic fluctuations induce highly varying food situations with predictable 'fat' and 'lean' periods for owls and Kestrels.

Owls and Kestrels mainly numerically responded to these fluctuating food conditions. Breeding percentage of Tengmalm's Owls *Aegolius funereus* in 500 nest boxes varied from 1% to 33% during 1973–2007 (Fig. 1 in Laaksonen *et al.* 2002). Breeding density of Kestrels varied from 0.9 to 11.7 nests/10 km² and that of Short-eared Owls *Asio flammeus* from 0 to 11.5 nests/10 km² during 1977–2007 (Table 2 in Korpimäki & Norrdahl 1991). Breeding densities of owls and Kestrels were positively correlated with the density indices of voles in the prevailing spring (Korpimäki 1994). Yearly mean clutch size of Tengmalm's Owls varied from 3.5 to 6.5 eggs and that of Kestrels from 4.3 to 6.0 eggs during

1977–2007 (Korpimäki & Hakkarainen 1991, Korpimäki & Wiehn 1998). Yearly mean clutch sizes of owls and Kestrels were closely correlated with vole density indices in current spring (Korpimäki & Hakkarainen 1991, Korpimäki & Wiehn 1998). The degree of hatching asynchrony of owl and Kestrels broods varied in the course of the vole cycles: it was less in low vole years than in increase and decrease vole years (Wiebe *et al.* 1998, Valkama *et al.* 2002).

Breeding dispersal of female Tengmalm's Owls was more extensive in the decrease than in the increase and low phases of the vole cycle, but this was not found for owl males (Korpimäki 1993), which mostly occupied the same territories after their first breeding attempts (Korpimäki 1988). Analyses of long-term dispersal and survival data from Kestrels showed largely similar results: more females returned to breed close to (<5 km) previous year breeding site in the increase than in the other phases of the vole cycle but no cycle-phase-related differences were found in males (Korpimäki *et al.* 2006, Vasko 2007). Annual adult survival of male Tengmalms's owls varied from approx. 25% to approx. 75% and was closely positively related to vole density indices in winter (Fig. 1 in Hakkarainen *et al.* 2002). Juvenile survival of Tengmalm's Owls was apparently higher in the increase phase than in the other phases of the vole cycle, because the proportion of fledglings that in subsequent years recruited to the breeding population was twice as high in the increase as in the other phases of the vole cycle (Korpimäki & Lagerström 1988). Similar results were also obtained for recruitment of Kestrel fledglings.

Male owls that initiated their breeding lifespan in the increase phase of the vole cycle had higher lifetime reproductive success (LRS) than those initiating their career in the decline phase (Korpimäki 1992). LRS of male owls was reduced in territories with higher proportion of farmland, mainly because their fledgling production was reduced in these territories in years when vole populations were declining (Hakkarainen *et al.* 2003, Laaksonen *et al.* 2004). LRS of male owls

increased with the proportion of old-growth forest in the territory, which appeared to be due to survival of males increasing with old forest in the territory (Laaksonen *et al.* 2004, Hakkarainen *et al.* 2008). Higher survival in old forests is likely to be due to better protection against larger birds of prey (e.g. Ural Owls *Strix uralensis* and Goshawks *Accipiter gentilis*), and/or to better availability of alternative prey (e.g. Bank Voles *Clethrionomys glareolus*, shrews, Willow Tits *Parus montanus* and Crested Tits *P. cristatus*, etc.), particularly in winter. In particular, Ural Owls have harmful effects on Tengmalm's Owls and thus decrease the habitat quality of smaller Tengmalm's Owls (Hakkarainen & Korpimäki 1996).

Temporal variation in vole abundance is the main determinant of breeding success, quality of offspring, survival of adult males, breeding dispersal distances, recruitment of offspring and LRS of Tengmalm's Owls. Since reduction in the area of old forests decreased the survival and LRS of Tengmalm's Owls, we predicted long-term declines of Tengmalm's owl populations in northern European boreal forests. This was also found in nation-wide monitoring study of birds of prey in Finland (Honkala & Saurola 2006). On the contrary, large-scale clear-cutting of North European boreal forests increases the grassy habitat for voles (Hakkarainen *et al.* 1996), which could benefit hunting Kestrels. A long-term increase in population size of Kestrels found in nation-wide monitoring study of birds of prey in Finland (Honkala & Saurola 2006) may thus be partly explained by changes in habitat structure. These results show that recent human-induced large-scale habitat manipulation can substantially alter the breeding population sizes and have profound effects on the composition of assemblages of birds of prey.

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