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Sex ratio and age structure of nomadic Tengmalm's owls: a molecular approach

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Sex ratio and age structure of Tengmalm's owls *Aegolius funereus* crossing the Gulf of Bothnia between Sweden and Finland were investigated by catching owls on the island of Stora Fjäderägg during autumn 1999. Using a molecular sexing technique, we investigated the assertions of previous studies that only adult female and juvenile Tengmalm's owls undertake nomadic movements. Juveniles were generally more frequent than adults, and the sex ratio of juvenile owls was significantly female-biased. However, contrary to expectation, adult males as well as females were caught. Additionally, among juveniles, males migrated earlier than females. Thus we infer that adult males as well as females are nomadic to some extent, and that the difference between the sexes in migratory habits is not as clear as previously thought.

Tengmalm's owl *Aegolius funereus* is a small nocturnal bird of prey with a Holarctic distribution, continuous within the Palaearctic boreal region (Mikkola 1983). It feeds mainly on voles (e.g. Korpimäki 1987a, Hörnfeldt et al. 1990), which in Fennoscandia show 3–4-year population cycles (see Stenseth 1999 for a recent review), and its breeding success varies considerably with the vole cycle. During years of low vole abundance, very few owls attempt to breed, and those that do produce few young (e.g. Korpimäki 1987b, Hörnfeldt et al. 1990). Vole cycles are not wholly synchronous over large areas (e.g. Steen et al. 1990, 1996), so on the scale of the Tengmalm's owl's distribution range the landscape can be considered to be spatially and temporally patchy with regard to food resources. Mysterud (1970) suggested that Tengmalm's owl is nomadic, settling to breed in areas where voles are temporarily abundant, and moving on when the vole population declines. According to Andersson (1980), nomadism is a favourable strategy for birds that experience cyclic fluctuations in food abundance, if the probability of breeding is increased by moving elsewhere. However, adult male Tengmalm's owls are territorial, and Lundberg (1979) suggested that territorial males might be under selective pressure to be resident, guarding their nest hole, irrespective of current vole abundance. For females and juveniles, on the other hand, nomadism or extensive natal dispersal would be favourable as an adaptation to periodic food scarcity (Lundberg 1979; see also Mysterud 1970). A number of studies have found support for Lundberg's hypothesis, though these are based on either museum specimens (Lundberg 1979) or ringing recovery data (Wallin and Andersson 1981, Löfgren et al. 1986, Korpimäki et al. 1987, Sonerud et al. 1988). In addition to being somewhat scanty, there is an inherent female-bias in ringing recovery data of Tengmalm's owl because a larger proportion of females than males is trapped for ringing/recovery during the breeding season. Korpimäki and Hongell (1986), in a 10-year study of irruptive Tengmalm's owls at a bird-ringing station in western Finland, found a higher overall proportion of adult females than males, also in support of Lundberg's (1979) hypothesis. However, owls were sexed using measurements of wing length and weight, which overlap between the sexes (Korpimäki and Hongell 1986, T. Hipkiss unpubl.), so their sex-ratio data are associated with a certain degree of uncertainty. In this study we used a molecular sexing technique combined with reliable criteria for ageing to accurately describe the sex ratio and age structure of Tengmalm's owls migrating across the Gulf of Bothnia between Sweden and Finland during a single autumn season.

Methods

Study area and fieldwork

Owls were trapped during autumn 1999 on Stora Fjäderägg, a small (1.8 × 1.3 km) island situated approximately 15 km from the Swedish mainland and 70 km from the Finnish mainland, in the Gulf of Bothnia (63°50′N, 21°00′E).

In this area of Sweden voles show 3–4-year population cycles of high amplitude (Hörnfeldt 1978, 1994).

During autumn 1999 vole numbers in Västerbotten, on the Swedish mainland (trapping area approx. 64°N, 20°E), had declined considerably after peaking in autumn 1998, and reached a low by spring 2000 (Hörnfeldt 2001). Breeding density of Tengmalm's owls was consequently high throughout spring 1999 but was at the low phase level in spring 2000 (B. Hörnfeldt, T. Hipkiss and U. Eklund unpubl.). In Lapua, southern Ostrobothnia, Finland (63°N, 21°E), voles peaked in autumn 1999 (Klemola et al. 2000, E. Korpimäki and K. Norrdahl pers. comm.). Breeding density of Tengmalm's owls in southern Ostrobothnia increased in 1999 after a low in 1998, and maintained the same density in 2000 (E. Korpimäki pers. comm.). Thus, vole and owl populations on the Swedish and Finnish mainland were in different phases.

We trapped migrating owls every night, from dusk until dawn, from 1 September until 17 October 1999. Trapping was avoided during strong winds and heavy rain. Trapping effort was constant when weather permitted, but duration of trapping increased with the seasonal increase in night length. Owls were caught in mist nets (16 mm mesh), and attracted by continuously playing a recording of the male's territorial call. All owls caught were aged by examining primary feather moult patterns (Hörnfeldt et al. 1988). A 50-µl blood sample was taken from the brachial vein under the wing, to be used for molecular sex determination (see below). Blood samples were stored in Queens College buffer (20% DMSO, 0.25M Na-EDTA, 100 mM Tris, pH 7.5, NaCl to saturation).

Molecular sexing

Sexing the owls relied on polymerase chain reaction (PCR) amplification of the sex-linked chromo-helicase-DNA binding genes *CHD1W* and *CHD1Z*, which map to the avian W and Z chromosomes respectively (Ellegren 1996, Griffiths et al. 1996, Griffiths and Korn 1997, Fridolfsson et al. 1998). The procedure was essentially carried out as described in Fridolfsson and Ellegren (1999) and Hörnfeldt et al. (2000), which can be referred to for a technical description. Females were characterized by displaying both a *CHD1W*-specific fragment (1.2 kb in size) and a shorter *CHD1Z*-specific fragment (0.7 kb), while males showed only the shorter Z-fragment.

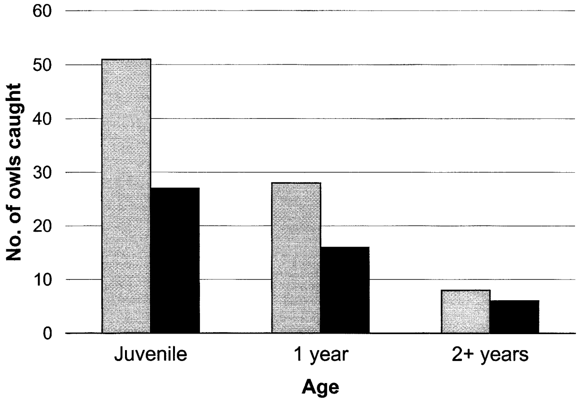

Fig. 1. Age and sex (female = grey bars, male = black bars) of Tengmalm's owls caught on Stora Fjäderägg during autumn 1999.

Results

We caught 143 Tengmalm's owls and 136 were successfully sexed. Juveniles were more frequent than adults, and the sex ratio of juveniles (65.4% female) differed significantly from parity ($\chi^2 = 6.78$, df = 1, n = 78, p = 0.01; Fig. 1). The sex ratios for the smaller samples of 1-yr-olds (63.6% female) and owls ≥ 2-yr old (57.1%) did not differ significantly from parity ($\chi^2 = 2.75$, df = 1, n = 44, p = 0.10 and $\chi^2 = 0.64$, df = 1, n = 14, p = 0.42, respectively; Fig. 1). The sex ratio did not differ significantly between age groups ($\chi^2 = 0.34$, df = 2, p = 0.84). Contrary to general expectations, adult males as well as females were caught. Four of the owls had previously been ringed at various locations in Finland. Two (a male and a female) had been ringed as nestlings (in 1998 and 1999), and one male had been ringed on migration during autumn 1999. One male individual had been ringed as a nestling in northwestern Finland in 1996 and had bred in Västerbotten, northern Sweden in spring 1999. Three owls ringed by us on Stora Fjäderägg were later caught during the same autumn; two females in Finland and one male in Sweden.

Playing a recording of the male's territorial call to attract Tengmalm's owls is a common method used at bird-ringing stations. To check whether this method had a stronger effect on one sex than the other, we examined the percentage of owls of each sex that we recaptured. If the skewed sex ratio of owls caught (64.0% female) was purely a result of an equal population sex ratio and females being more strongly attracted to the tape recording, then more females than males would be recaptured and the sample would be even more female-biased than that of the owls caught initially. Seven females and four males (63.6% female) were recaptured, corresponding to a recapture rate of 8.0% for females and 8.2% for males. The sex ratio of recaptured owls was not significantly different from that of the initial catch ($\chi^2 = 0.08$, df = 1, n = 11, p = 0.78), and suggests that the skewed sex ratio in the initial catch was indeed representative of the actual population sex ratio.

Median trapping date was significantly later for juvenile females than for juvenile males (Mann-Whitney U-test: $U = 311.5$, $n = 78$, $p < 0.001$), but there was no significant difference between sexes for adults ($U = 378.5$, $n = 58$, $p = 0.78$). Tengmalm's owls were caught throughout the night, with peaks after dusk and between 23.00 and midnight. Median trapping time did not differ significantly between the sexes for juveniles ($U = 687.0$, $n = 78$, $p = 0.91$) or adults ($U = 367.0$, $n = 58$, $p = 0.64$).

Discussion

Our data suggest that sex and age differences in migratory tendency in Tengmalm's owl might not be as clear-cut as previously thought. That we caught adult males was unexpected since breeding males are not considered to be itinerant (Lundberg 1979, Löfgren et al. 1986, Korpimäki et al. 1987). Most (73%) of the adult males were one year old. Few males breed in their first year (Korpimäki 1988a), although the number is higher during peak vole years (Korpimäki 1988a, Hörnfeldt et al. 1990). Thus, it is likely that many of these 1-yr old males had not yet bred, and were searching for a suitable territory. However, it is less likely that the older individuals ($\geq$2-yr old) had never established territories or bred. Indeed, we trapped one male on Stora Fjäderägg that had bred previously, approximately 50 km from the island. Löfgren et al. (1986) and Korpimäki et al. (1987) reported similar findings of males later recovered far from their breeding territory, but did not consider them to be nomadic (sensu Andersson 1980), since they were not recovered at subsequent breeding sites. However, these individuals were clearly not resident or defending their territory, as predicted by Lundberg's (1979) hypothesis. Löfgren et al. (1986) also reported a male moving 21 km between breeding sites used in different years but did not consider this shift far enough to be classified as nomadism. However, these territories were certainly too far apart to be considered as neighbouring, in contrast to those used by polygynously breeding males (e.g. Carlsson et al. 1987), and such a male would still have to familiarize himself with the new area to breed successfully (cf. Korpimäki 1987c). Although males may be under selective pressure to remain on the same territory throughout their life (Lundberg 1979), this may vary according to territory quality. A male on a low-quality territory may benefit from searching for a better territory when vole populations decline (but see Korpimäki 1988b). Additionally, selection for nomadism might increase with increasing latitude, owing to more pronounced vole cycles and increased snow depth in winter making male residency less favourable at the most northerly latitudes (Korpimäki 1986).

Juveniles were trapped more frequently than adults, as also Korpimäki and Hongell (1986) found in their study on irruptive owls. However, in addition we found a clear female-biased juvenile sex ratio. Recovery rate of breeding owls ringed as nestlings also suggests that natal dispersal is more extensive among females than males (Löfgren et al. 1986, Korpimäki et al. 1987, Sonerud et al. 1988), which is a common pattern in birds, particularly those with resource defence polygynous mating systems (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997). Here we also report a temporal difference in male and female natal dispersal, with males being caught earlier than females, not previously described in Tengmalm's owl. Differential timing of autumn migration with respect to age and sex is complex, and patterns vary among species and are not necessarily dependent on the extent of dispersal (Gauthreaux 1982). In Tengmalm's owl it is possible that juvenile males are driven away early from their natal territory by the resident male (their 'father'), since they might be regarded as competitors (cf. Gauthreaux 1978). Juvenile females might be tolerated for longer and disperse at a later date. Alternatively, as Tengmalm's owls start breeding early in the year, it would be advantageous for young males to start searching for a territory as early as possible, ahead of their competitors (cf. Myers 1981).

The present data and a reinterpretation of previously published data suggest that adult nomadism is to be expected not only in female but also in male Tengmalm's owls. While the overall higher trapping frequency of females, particularly among juveniles, suggests that they are more itinerant than males, it might alternatively represent a female-biased population sex ratio. For instance, the sex ratio of Tengmalm's owl broods in northern Sweden during 1998 was significantly male-biased (Hörnfeldt et al. 2000). If brood sex ratio varies with, for example, fluctuations in vole abundance or some other environmental factor, and is sometimes female-biased, then this could produce the high frequency of itinerant females presented here. We acknowledge that our results should ideally be backed up with similar data collected during several years, to reveal if the sex ratio and age structure of nomadic Tengmalm's owls vary during the vole cycle. A complete study of Tengmalm's owl sex ratio and age structure at breeding sites and on migration, using a molecular approach, would be required to fully describe the autumn movements of this species.

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