ORIGINAL ARTICLE

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High interannual variation in the hatching sex ratio of Tengmalm's owl broods during a vole cycle

Abstract The sex ratio at hatching in broods of Tengmalm's owl (*Aegolius funereus*) in northern Sweden was investigated for 3 years characterized by different phases of the vole and owl cycle. Previous work showed the sex ratio in this species to be male-biased for 1 year with a favourable food supply, and that in feeding experiments male nestlings (but not females) suffered higher mortality when food was limited, but not otherwise. Here we present data from a complete 3-year owl cycle, showing that mean brood sex ratio varied significantly among years, being male-biased (65% males) in the first year of high owl breeding density, unbiased (49%) in the second year of high owl breeding density, and female-biased (33% males) in the owls' low year. Brood sex ratio did not vary significantly within years with laying date or parental age. Vole availability, and therefore the owls' food supply, declined during the 3 years studied. Tengmalm's owl parents thus appear to adaptively adjust the sex ratio of their broods according to the expected annual mortality risk of sons.

Keywords *Aegolius funereus* · Brood sex ratio · Food supply · Sex-biased mortality · Vole-predator cycles

Introduction

Natural selection usually favours a population with an equal number of males and females (Fisher 1930). However, when the relative fitness of males and females varies under different circumstances, it is adaptive for individual parents to invest more in the sex whose fitness is expected to be highest (Trivers and Willard 1973; Charnov 1982; Frank 1990; Hasselquist and Kempenaers 2002). Recent

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studies on birds provide convincing evidence that parents bias the sex ratio of their broods at hatching in favour of the sex that benefits most from being reared under the current socio-environmental circumstances (e.g. Komdeur et al. 1997; Nager et al. 1999; Sheldon et al. 1999). In sexually size-dimorphic species, one sex often suffers from higher mortality when environmental conditions are poor. Often the larger sex suffers because it has higher energy requirements during growth (Clutton-Brock et al. 1985; Røskaft and Slagsvold 1985; Griffiths 1992), although sometimes the smaller sex suffers because of being dominated by larger siblings of the opposite sex (Anderson et al. 1993; Hipkiss et al. 2002a). When condition-dependent differential mortality exists between the sexes, parents ought to bias the sex ratio of their broods towards the sex that enjoys the lower mortality risk under the current circumstances. A number of avian studies indeed show sex allocation favouring the sex with the lowest mortality risk (Kilner 1998; Torres and Drummond 1999; Nager et al. 1999; Kalmbach et al. 2001).

Tengmalm's owl (*Aegolius funereus*) is a nocturnal hole-nesting raptor with a Holarctic boreal distribution (Mikkola 1983) that feeds mainly on voles (Korpimäki 1988; Hörnfeldt et al. 1990). In northern Fennoscandia 3–4 year cyclic fluctuations in vole abundance affect the owl's breeding strategy and success (e.g. Korpimäki 1987; Hörnfeldt et al. 1990), so that owl cycles, synchronous with those of voles, can be identified. Owl cycles in northern Sweden have been characterized by 2 consecutive years of relatively high owl breeding density followed by a year of very low owl breeding density (Hörnfeldt et al. 1990). Even breeding parameters such as laying date and clutch size vary regularly with cyclic vole abundance (Korpimäki 1987; Hörnfeldt et al. 1990). Tengmalm's owl females are around 5% larger than males outside the breeding season (Hipkiss 2002), and this size difference is reflected in nestlings (Hipkiss et al. 2002a). As in many other raptors, the young hatch asynchronously (at intervals of 1–2 days) and the youngest often die before fledging (cf. Newton 1979; Mikkola 1983). Supplemental feeding experiments

during 2 years of high owl breeding density showed that male nestlings suffered higher mortality than females when the natural food supply was relatively more limited, but not otherwise (Hipkiss et al. 2002a). This was attributed to males being dominated by their larger sisters (cf. Anderson et al. 1993). Thus, mortality risk for male nestlings varied with food availability, and this mortality risk is likely to be highest in the low phase of the owl-vole cycle. Brood sex ratios of Tengmalm's owls in northern Sweden were highly male-biased during a single year with a favourable natural food supply (Hörnfeldt et al. 2000); however, brood sex ratio data from more than 1 year in a vole-predator cycle have previously not been published for this or any other avian predator. In years with a less favourable food supply, when sons are expected to suffer from increased mortality, we might also expect parents to invest more in daughters. Studies on raptors show that brood sex ratios in a number of species vary adaptively with laying date (e.g. Dijkstra et al. 1990; Zijlstra et al. 1992). Parents produce an excess of the sex that benefits most from hatching at a particular time during the breeding season, often according to its prospects of breeding as a yearling (Daan et al. 1996). Here we show that the sex ratio at hatching in broods of Tengmalm's owl varies during the course of an owl cycle, according to the expected mortality risk of sons, but that there is no significant variation within years with laying date.

Materials and methods

The study was carried out in Västerbotten, northern Sweden (approx. 64°N, 20°E), an area situated within the middle boreal vegetation zone (Ahti et al. 1968). Between 1998 and 2000 nearly 300 nest boxes (20 × 20 cm base, 8.5-cm-diameter entrance hole), placed in trees along roads at approx. 1 km intervals, were inspected every 3–4 weeks, from March to June, to detect nesting Tengmalm's owls. Nests were revisited when hatching was expected (28–30 days after laying) and frequently afterwards to record brood size. The laying date of each detected clutch was estimated by backdating, using a laying interval of 2 days, or by ageing the oldest nestling using its wing length and assuming an incubation period of 29 days (Carlsson and Hörnfeldt 1994). Nestlings were ringed, initially with individually coloured plastic rings, then later with standard aluminium rings. Hatching position of nestlings was determined by frequent nest box inspections during the hatching period, and by relative size differences among asynchronously hatched nestlings. We attempted to catch both parent birds at each nest. Adult females from all nests were caught by hand during the day whilst brooding; adult males were caught from 95% of successful nests, using traps attached to nest boxes, at night when they visited the nest box to feed their nestlings. Parent birds were ringed and aged using moult patterns of primaries (Hörnfeldt et al. 1988).

A 50-μl blood sample was taken from each nestling by brachial vein puncture, 1–3 days after hatching, for molecular sexing. Broods that were abandoned by their parents before hatching was complete ($n=11$), or in which more than one egg failed to hatch ($n=7$), were not included in the statistical analysis of brood sex ratios. However, in 2000, when few owls bred and sample size was low, two nests with incomplete clutches (two eggs in each nest failed to hatch) were included. These four eggs, as well as four from an abandoned clutch were collected to provide additional material for sexing. The augmented sample of clutch sex ratios for 2000 was used to validate the hatching sex ratio for this year, but was not itself used in any analyses. Sex determination of nestlings relied on polymerase chain reaction (PCR) amplification of one intron from the sex chromosome linked *CHD1* gene, which in birds differs in size between the Z and W chromosomes (Fridolfsson and Ellegren 1999). Females were characterized by displaying both a 1.2 kb W-specific fragment and a 0.7 kb Z-specific fragment, while males showed only the shorter Z-fragment (Fridolfsson and Ellegren 1999).

The differences in mean brood sex ratios at hatching among the 3 years, and interactions with other variables were analysed in generalized linear models using binomial error distributions and logit link functions (Crawley 1993), using GLIM version 4.09. Analyses were performed at the brood level, i.e. with brood size as the binomial denominator. Female identity was included in the model, to account for the five females that were observed during more than 1 year. The effect of year, Julian laying date, maternal age and paternal age were analysed, together with the interaction terms between year and the other variables. We used two age categories; yearlings and 2-year-olds or older. Models were corrected for overdispersion, using the method of Williams (1982), and validity was confirmed by visual inspection of residuals (Crawley 1993). We also checked for any sex bias in the hatching sequence by comparing the median hatching position, for all broods combined, each year for males and females. Similar generalized linear models were used to test whether brood sex ratio within years was significantly biased. Proportion of males in observed broods was tested against a predicted mean value of 50% males for matching brood sizes.

Indices of natural food supply for the owls were obtained from a running survey (within the Swedish Environmental Protection Agency's National Environmental Monitoring Programme) of small mammals in which snap-trapping has been carried out twice yearly since 1971. Sampling was carried out for three consecutive nights in spring (late May) and autumn (late September) in 58 regularly distributed 1-ha plots in an area including the owl study site (see Hörnfeldt 1978, 1994, 2004 for details). The pooled number of voles (*Clethrionomys glareolus*, *C. rufocanus*, and *Microtus agrestis*) trapped per 100 trap-nights was used as an index of food supply in spring and autumn. A summer vole index, reflecting the post-fledging food supply, was calculated as the

mean of the spring and autumn vole trapping indices. Winter decline in vole numbers, which reflects the stability of the owls' food supply prior to the breeding season, was calculated as the percentage decrease in the vole index from autumn to the following spring.

Results

Mean brood sex ratio at hatching was significantly different during the 3 years studied (Table 1, Fig. 1), each characterized by a different phase of the owl cycle, and hence food supply. The total number of Tengmalm's owl nests in our nest boxes was 41 in 1998, 61 in 1999 and 8 in 2000. The spring vole index declined from 1.39 in 1998, through 1.34 in 1999, to 0.23 in 2000. The derived summer vole index, which reflects the food supply post-fledging, declined from 5.58 in 1998, through 2.23 in 1999, to 1.63 in 2000. In addition, the winter decline in vole numbers increased from 34% in 1998, through 86% in 1999, to 93% in 2000. Thus the owls' food supply prior to, during and after breeding deteriorated from 1998 to 2000, and was reflected by the owls' mean clutch size decreasing from 6.4 in 1998, through 5.6 in 1999 to 3.5 in 2000 (one-way ANOVA, $F=19.8$; $n=92$; $P<0.01$). In 1998, the first year of high owl breeding density, the mean brood sex ratio at hatching was significantly male-biased (65%, $n=24$, $\chi_1^2=7.23$, $P<0.01$; see also Hörnfeldt et al. 2000). In 1999, the second year of high owl breeding density, the mean brood sex ratio at hatching was unbiased (49%, not significantly different from 50%, $n=43$, $\chi_1^2<0.01$, $P=0.96$). In contrast, in 2000, the owls' low year, mean brood sex ratio was significantly female-biased (33%, $n=6$, $\chi_1^2=4.67$, $P<0.03$). The mean sex ratio in clutches in 2000 was also female-biased (35%, $n=7$, $\chi_1^2=5.94$, $P=0.01$). To summarize, brood sex ratio at hatching clearly declined with food supply, and hence varied in line with the expected mortality risk of sons. Brood sex ratio did not significantly vary with laying date or parental age, and there was no significant interaction between these variables and year (Table 1). Median hatching position for all broods combined did not differ between the sexes in 1998 (Mann-Whitney $U=2078.0$, $n=138$, $P=0.78$), 1999 ($U=6005.5$, $n=231$, $P=0.19$) or 2000 ($U=13.5$, $n=15$, $P=0.15$).

Table 1 Results of log-likelihood ratio tests (*LLR*) of the effects of year, laying date and parental age on the hatching sex ratio of 73 Tengmalm's owl broods during 1998–2000

	LLR	df	P
Year	13.83	2	< 0.01
Laying date	0.80	1	0.37
Maternal age	0.26	1	0.61
Paternal age	0.46	1	0.50
Year × laying date	1.68	2	0.43
Year × maternal age	0.09	2	0.95
Year × paternal age	0.35	2	0.85

Discussion

Our data on the sex ratio at hatching of Tengmalm's owl broods showed high interannual variation during an owl cycle, switching from a male bias in the first year of high breeding density, followed by an unbiased sex ratio in the second year of high breeding density, and finally a female bias in the owls' low year (Fig. 1). While in a number of other raptorial birds brood sex ratio varies with laying date (e.g. Dijkstra et al. 1990; Zijlstra et al. 1992), we did not observe this in Tengmalm's owl. In raptors where sex ratio and laying date co-vary, the prospective breeding success of one sex is disproportionately influenced by its fledging date (Daan et al. 1996). While laying date affects breeding success (in terms of clutch size) of individual Tengmalm's owls, the effect of year is greater (Hörnfeldt et al. 1990). In addition, although breeding performance of Tengmalm's owls improves with age, the effect of year is generally more important (Laaksonen et al. 2002), and we found no evidence that parental age affected the brood sex ratio. The breeding biology of Tengmalm's owl is very flexible and well adapted to the vole cycles it experiences in northern Scandinavia. Traits such as clutch size and laying date are strongly influenced by vole abundance (Korpimäki 1987; Hörnfeldt et al. 1990) and fluctuate in a similar regular manner. Consequently, it is not surprising that phase of the vole cycle, characterized by different vole abundance, appears to be the most important potential influence on brood sex ratio variation, rather than laying date or parental age. Other avian predators of voles show brood sex ratio variation with fluctuations in small rodent abundance (Wiebe and Bortolotti 1992; Appleby et al. 1997; Korpimäki et al. 2000; Brommer et al. 2003; but see Leroux and Bretagnolle 1996). However, in these studies males were the most frequent sex when food conditions were
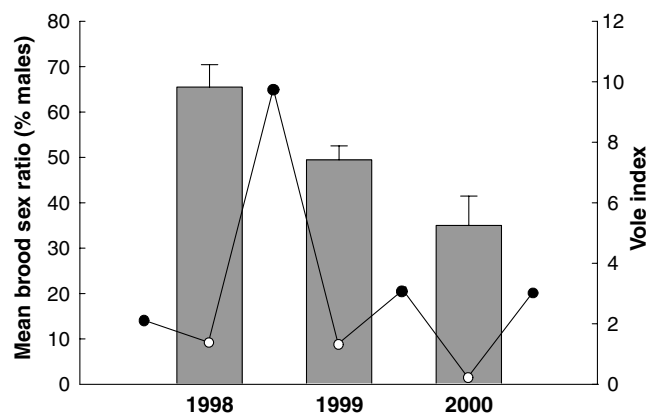

Fig. 1 Mean sex ratio (per cent males) at hatching in Tengmalm's owl broods (*grey bars*; *error bars* represent + 1 SE) and vole trapping index (*line*; voles trapped/100 trap-nights) in spring (*white circles*) and autumn (*black circles*). 1998 ($n=24$ broods) and 1999 ($n=43$) represent first and second years of high owl breeding density; 2000 ($n=6$) represents year of low owl breeding density

unfavourable, contrary to our results for Tengmalm's owl. In Ural owls (*Strix uralensis*), brood sex ratio at hatching was male-biased for 3 consecutive years characterized by the authors as having low vole abundance. However, the authors could find no evidence of any mortality difference between males and females, or provide any other explanation for food-dependent sex allocation (Brommer et al. 2003). In American and European kestrels (*Falco sparverius* and *F. tinnunculus* respectively), brood sex ratios halfway through the nestling stage were male-biased in years of food scarcity and neutral in other years (Wiebe and Bortolotti 1992; Korpimäki et al. 2000). In both cases, it was suggested that parents were unable to produce females (the larger, and assumed by the authors to be the most expensive sex) when food was scarce. In tawny owls (*Strix aluco*), brood sex ratios around 1 week after hatching were more female-biased in territories with more abundant prey. The reproductive success of females, but not males, depended on the abundance of prey on their natal territory at the time of fledging (Appleby et al. 1997).

The high interannual variation in mean brood sex ratio at hatching, in line with predicted mortality risk of males, suggests that this trait is adaptive. In supplementary feeding experiments, Tengmalm's owl nestlings showed condition-dependent differential mortality, with males suffering from higher mortality than females when natural food supply was limited, but not otherwise (Hipkiss et al. 2002a). In a number of other birds with sex-biased mortality patterns, parents produce sex-biased clutches in favour of the sex with the lowest mortality risk (Kilner 1998; Torres and Drummond 1999; Nager et al. 1999; Kalmbach et al. 2001). Supplementary-fed Tengmalm's owls showed lower male nestling mortality in 1998, when voles were more stable during the preceding winter and increased substantially throughout the breeding season, compared with 1999, when vole availability was lower (Hipkiss et al. 2002a). Food availability during the owls' breeding season in 2000 (the owls' low phase) was lower still, so mortality risk for male nestlings was probably even higher than during 1999. Producing female-biased clutches would prevent unnecessary loss of male nestlings during the relative food shortage at that time. Parents biased the sex ratio of their broods in favour of females when high male mortality was most likely (the owls' low year), and instead produced more males when their mortality risk was lowest (the first year of high breeding density).

Energy expenditure during breeding is often higher in adult male raptors than in females (Wijnandts 1984; Masman et al. 1988), and fledging success depends very much on the male's hunting success (Masman et al. 1989). Male Tengmalm's owls show great variation in reproductive success, with a small proportion of individuals being polygynous (Carlsson et al. 1987; Korpimäki 1989), while most are monogamous or even lack a mate (Hakkarainen and Korpimäki 1998). If sons, as a consequence of their demanding ecological role and high reproductive potential, benefit more from a good start in life than daughters, then the interannual brood sex ratio adjustments in Tengmalm's owl might provide additional fitness returns to parents (cf. Trivers and Willard 1973; Appleby et al. 1997). This might be another reason why parents invest in sons during the year with the most favourable food supply.

Here we present data showing that the mean annual brood sex ratio changed markedly during the 3 years studied. However, it would be interesting to examine the sex ratio of broods produced by individual females that bred in more than 1 year. This would reveal whether individual females really do adjust the brood sex ratio according to vole availability, or if different females with fixed brood sex ratio strategies breed during different phases of the vole cycle (cf. Oddie and Reim 2002). We observed only five females for more than 1 year. Four females observed in both 1998 and 1999 showed varying sex allocation strategies during the 2 years, but with no clear pattern for all four females. However, a single female observed breeding during the entire 3-year study period laid clutches with sex ratios biased in the same direction as the annual means (100, 40 and 20% males in 1998, 1999 and 2000 respectively). Another interesting observation was that of a sequentially polyandrous female in 1998, who lay clutches with 80 and 83% males in her first and second clutches, respectively. These observations suggest that individual Tengmalm's owl females are indeed able to adjust the sex ratio of their clutch according to current phase of the vole cycle and expected mortality risk of sons. However, a study consisting of several individuals repeatedly observed during consecutive years would be necessary to confirm this assertion, as Oddie and Reim (2002) were able to in their study of great tits (*Parus major*).

As far as we know, this study is the only one in which hatching sex ratio of an avian vole predator from a whole vole cycle has been studied. Thus, we do not know if the interannual variation presented here is temporally and geographically general for Tengmalm's owls experiencing vole cycles. Annual variation in brood sex ratios coupled with annual variation in breeding success in Tengmalm's owls has potentially interesting implications for the population sex ratio in this species. Since males were favoured in the year of highest breeding success, while females were favoured in the year of lowest breeding success, the population sex ratio could potentially become highly male-biased. Such a scenario would favour parents producing broods in favour of the rarer sex (cf. Fisher 1930). However, we have no reliable data on post-fledging or adult mortality, or on the population sex ratio in Tengmalm's owl. For example, higher adult mortality, especially in the low phase of voles and among site-tenacious males, might negate any potential excess of males in the population. In addition, Tengmalm's owl is nomadic; particularly juveniles and adult females tend to migrate when food supply declines (e.g. Löfgren et al. 1986; Hipkiss et al. 2002b), and intermixing of individuals from wide areas with different vole

dynamics might contribute to prevent any significant bias in the population sex ratio within any particular area.

We detected no clear difference in the median hatching position of male and female nestlings. Biasing the laying order of eggs according to their sex, so that the preferred, fittest sex hatches earlier while the other, least fit sex hatches later, is a potential mechanism of sex ratio adjustment in birds with asynchronously hatching broods exhibiting brood reduction (e.g. Dijkstra et al. 1990; Blanco et al. 2002). While the underlying physiological mechanism of sex ratio adjustment is unknown (Pike and Petrie 2003), Tengmalm's owl in general shows remarkable flexibility in its ability to respond to its cyclic food supply, and adjusting the brood sex ratio according to the expected mortality risk of sons allows the owl to fine-tune the fitness value of its brood according to current environmental circumstances.

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5:169–211

Anderson DJ, Budde C, Apanius V, Gomez JEM, Bird DM, Weathers WW (1993) Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). Ecology 74:367–376

Appleby BM, Petty SJ, Blakey JK, Rainey P, MacDonald DW (1997) Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? Proc R Soc London B Biol Sci 264:1111–1116

Blanco G, Dávila JA, López Septiem JA, Rodríguez R, Martínez F (2002) Sex-biased initial eggs favours sons in the slightly size-dimorphic scops owl (*Otus scops*). Biol J Linn Soc 76:1–7

Brommer JE, Karell P, Pihlaja T, Painter JN, Primmer CR, Pietiäinen H (2003) Ural owl sex allocation and parental investment under poor food conditions. Oecologia 137:140–147

Carlsson B-G, Hörnfeldt B (1994) Determination of nestling age and laying date in Tengmalm's owl: use of wing-length and body mass. Condor 96:555–559

Carlsson B-G, Hörnfeldt B, Löfgren O (1987) Bigyny in Tengmalm's owl *Aegolius funereus*: effect of mating strategy on breeding success. Ornis Scand 18:237–243

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133

Crawley MJ (1993) GLIM for ecologists. Blackwell, Oxford

Daan S, Dijkstra C, Weissing FJ (1996) An evolutionary explanation for seasonal trends in avian sex ratios. Behav Ecol 7:426–430

Dijkstra C, Daan S, Buker JB (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. Funct Ecol 4:143–147

Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford

Frank SA (1990) Sex allocation theory for birds and mammals. Annu Rev Ecol Syst 21:13–55

Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Griffiths R (1992) Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. Ibis 134:237–244

Hakkarainen H, Korpimäki E (1998) Why do territorial male Tengmalm's owls fail to obtain a mate? Oecologia 114:578–582

Hasselquist D, Kempenaers B (2002) Parental care and adaptive brood sex ratio manipulation in birds. Phil Trans R Soc London B Biol Sci 357:363–372

Hipkiss T (2002) Sexual size dimorphism in Tengmalm's owl (*Aegolius funereus*) on autumn migration. J Zool (London) 257:281–285

Hipkiss T, Hörnfeldt B, Eklund U, Berlin S (2002a) Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. J Anim Ecol 71:693–699

Hipkiss T, Hörnfeldt B, Lundmark Å, Norbäck M, Ellegren H (2002b) 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

Hörnfeldt B (1994) Delayed density dependence as a determinant of vole cycles. Ecology 75:791–806

Hörnfeldt B (2004) Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. Oikos (in press)

Hörnfeldt B, Carlsson B-G, Nordström Å (1988) Molt of primaries and age determination in Tengmalm's owl (*Aegolius funereus*). Auk 105:783–789

Hörnfeldt B, Carlsson B-G, Löfgren O, Eklund U (1990) Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). Can J Zool 68:522–530

Hörnfeldt B, Hipkiss T, Fridolfsson A-K, Eklund U, Ellegren H (2000) Sex ratio and fledging success of supplementary-fed Tengmalm's owl broods. Mol Ecol 9:187–192

Kalmbach E, Nager RG, Griffiths R, Furness RW (2001) Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. Proc R Soc London B Biol Sci 268:2175–2179

Kilner R (1998) Primary and secondary sex ratio manipulation by zebra finches. Anim Behav 56:155–164

Komdeur J, Daan S, Tinbergen J, Mateman C (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525

Korpimäki E (1987) Timing of breeding of Tengmalm's owl *Aegolius funereus* in relation to vole dynamics in western Finland. Ibis 129:58–68

Korpimäki E (1988) Diet of breeding Tengmalm's owls *Aegolius funereus*: long-term changes and year-to-year variation under cyclic food conditions. Ornis Fenn 65:21–30

Korpimäki E (1989) Mating system and mate choice of Tengmalm's owls *Aegolius funereus*. Ibis 131:41–50

Korpimäki E, May CA, Parkin DT, Wetton JH, Wiehn J (2000) Environmental- and parental condition-related variation in sex ratio of kestrel broods. J Avian Biol 31:128–134

Laaksonen T, Korpimäki E, Hakkarainen H (2002) Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. J Anim Ecol 71:23–31

Leroux A, Bretagnolle V (1996) Sex ratio variations in broods of Montagu's harriers *Circus pygargus*. J Avian Biol 27:63–69

Löfgren O, Hörnfeldt B, 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

Masman D, Daan S, Beldhuis HJA (1988) Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. Ardea 76:64–81

Masman D, Dijkstra C, Daan S, Bult A (1989) Energetic limitation of avian parental effort: field experiments in the kestrel (*Falco tinnunculus*). J Evol Biol 2:435–455

Mikkola H (1983) Owls of Europe. Poyser, London

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R (1999) Experimental demonstration that offspring sex ratio varies with maternal condition. Proc Natl Acad Sci USA 96:570–573

Newton I (1979) Population ecology of raptors. Poyser, London

Oddie KR, Reim C (2002) Egg sex ratio and paternal traits: using within-individual comparisons. Behav Ecol 13:503–510

Pike TW, Petrie M (2003) Potential mechanisms of avian sex manipulation. Biol Rev 78:553–574

Røskaft E, Slagsvold T (1985) Differential mortality of male and female offspring in experimentally manipulated broods of the rook. J Anim Ecol 54:261–266

Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J (1999) Ultraviolet colour variation influences blue tit sex ratios. Nature 402:874–877

Torres R, Drummond H (1999) Variably male-biased sex ratio in a marine bird with females larger than males. Oecologia 118:16–22

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Wiebe KL, Bortolotti GR (1992) Facultative sex ratio manipulation in American kestrels. Behav Ecol Sociobiol 30:379–386

Wijnandts H (1984) Ecological energetics of the long-eared owl (*Asio otus*). Ardea 72:1–92

Williams DA (1982) Extra-binomial variation in logistic linear models. Appl Stat 31:144–148

Zijlstra M, Daan S, Bruinenberg-Rinsma J (1992) Seasonal variation in the sex ratio of marsh harrier *Circus aeruginosus* broods. Funct Ecol 6:553–559