

Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings

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Summary

1. In sexually size-dimorphic birds, the larger sex requires more energy during growth, and often suffers from a higher mortality risk during growth than the smaller one when food is limited.
2. Sex-specific growth and mortality were examined in Tengmalm's owl *Aegolius funereus* (L.) nestlings, a species in which adult females are slightly larger than males. Nestlings were unambiguously sexed using molecular techniques. Nestling mortality in broods provided with supplemental food was compared with that in controls in an experiment carried out during two breeding seasons, 1998 and 1999.
3. The natural food supply during the two years of the experiment differed. Although the spring vole abundance was similar for the two years, 1998 was characterized by a less severe decline in vole abundance during the previous winter, and also a greater increase in vole abundance during the summer than 1999. It was consequently inferred that the owls' natural food supply was more limited in 1999.
4. In 1998, female nestlings attained a 5% higher asymptotic mass than males, and fed nestlings were heavier than controls. No difference in rate of mass gain or wing growth was detected.
5. Overall mortality was lower in fed broods than controls in 1999 only. Unexpectedly, female nestling mortality was unaffected by supplemental feeding during both years. However, in 1999, when natural food supply was more limited, male nestling mortality was reduced in supplementary-fed broods.
6. It is suggested that the females' larger size gives them a competitive advantage against their male siblings when fighting over food items, and that when food is limited, males rather than females suffer increased mortality owing to lack of food.
7. This study illustrates the importance of repeating food supplementation experiments to account for annual variation in natural food supply.

Key-words: cyclic vole abundance, differential mortality, nestling mass, repeated feeding experiment, sibling aggression.

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Introduction

In sexually size-dimorphic species, in which one sex is larger than the other, size difference in adults can be attained by difference in the rate and/or duration of growth at the juvenile stage (Martin, Willner & Dettling 1994). In sexually size-dimorphic birds,

the larger sex usually grows at a faster absolute rate (Teather & Weatherhead 1994), and consequently requires more energy during growth (Lindén 1981; Fiala & Congdon 1983; Slagsvold, Røskaft & Engen 1986; Teather & Weatherhead 1988; Anderson *et al.* 1993b). The greater food requirements of the larger sex render it more susceptible to food shortage and other hardships, leading to increased mortality during periods of extreme environmental stress (Clutton-Brock, Albon & Guinness 1985; Weatherhead & Teather 1991). A number of studies lend support to

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this, with the larger sex suffering higher mortality than the smaller one, or sex ratios being biased towards the smaller sex, when food was limited generally (e.g. Teather & Weatherhead 1989) or when breeding success was low (e.g. Hörnfeldt, Hipkiss & Eklund 2001). In some asynchronously hatching species, differential mortality of the larger sex under harsh environmental conditions is only apparent in the last-hatched nestling (Røskaft & Slagsvold 1985; Griffiths 1992; Torres & Drummond 1997).

Tengmalm's owl *Aegolius funereus* (L.) is a small nocturnal raptor of the Holarctic coniferous belt (Mikkola 1983). It feeds mainly on voles (Korpimäki 1988; Hörnfeldt *et al.* 1990), which in northern Sweden undergo population cycles of 3–4 years (Hörnfeldt 1978, 1994), and fluctuations in their abundance affect much of its breeding biology and success (Korpimäki 1987a; Hörnfeldt *et al.* 1990). As in many other raptors, eggs are laid at intervals of about 2 days, and incubation begins after the first or second egg is laid, so the nestlings hatch asynchronously and the youngest suffer from a higher mortality risk owing to a combination of starvation and sibling aggression (Newton 1979; Mikkola 1983). Adult Tengmalm's owls are sexually size-dimorphic, females weighing around 5% more than males outside the breeding season (Hipkiss 2002), though they are much heavier during breeding, even after laying (Korpimäki 1990). This sexual size dimorphism prompted Hörnfeldt *et al.* (2000) to investigate the effects of extra food on the change in brood sex ratio between hatching and fledging in Tengmalm's owl. The authors expected that, owing to sexual size dimorphism, mortality of female nestlings would be reduced in broods provided with supplemental food, leading to brood sex ratios being more female-biased at fledging in fed broods than in control broods. However, supplemental feeding had no effect on fledging sex ratios or on fledging success in general, and it was concluded that the natural food supply was too good to reveal any effects of extra food. In addition, growth data on Tengmalm's owl nestlings were not presented, so it was not possible to assess sexual size dimorphism in nestlings. Here we extend the feeding experiment carried out by Hörnfeldt *et al.* (2000), by repeating it during the subsequent year, characterized by a different phase in the vole population cycle. When natural food supply varies greatly it is particularly important to perform food supplementation experiments at different levels of natural food abundance, and to record these background control conditions (Hairston 1989; Boutin 1990). Field experiments are rarely repeated, and frequently give different results owing to environmental variation (Hairston 1989). We examined the effect of supplemental feeding on the mortality of male and female Tengmalm's owl nestlings in interaction with the effect of year, and vole abundance was monitored to assess the natural food supply. We also examined growth patterns of male and female

nestlings, to measure the degree of sexual size dimorphism at this stage.

Materials and methods

GENERAL FIELDWORK

The study area was situated in Västerbotten, northern Sweden (approx. 64°N, 20°E). This area is located within the middle boreal vegetation zone (Ahti, Hämet-Ahti & Jalas 1968) and is dominated by managed coniferous forest with small areas of low-intensity agriculture. During 1998 and 1999, nearly 300 nest-boxes (20 × 20 cm base, 8.5 cm diameter entrance hole), placed along roads at approx. 1-km intervals, were inspected every 3–4 weeks, from March to June, to detect nesting Tengmalm's owls. The laying date of each detected clutch was estimated by backdating. If the clutch was discovered during laying, a laying interval of 2 days per egg was used, and if the clutch was discovered later, the wing-length of the oldest nestling was measured to determine its age, and an incubation period of 29 days was assumed (Carlsson & Hörnfeldt 1994). Nests were revisited when hatching was expected (28–30 days after laying), and data were collected on clutch size, brood size and hatching order. Nestlings were ringed, initially with individually coloured plastic rings, and subsequently with standard aluminium rings, so that they could be identified during the entire period in the nest. Nestling mortality was recorded by frequent observation and after fledging by X-raying nestbox remains to detect aluminium rings from dead nestlings.

FEEDING EXPERIMENT

Every second brood discovered was provided with additional food during the entire nestling period (from when the first nestling hatched until the last fledged). The remaining broods were designated as controls, but were monitored in an identical manner to the fed broods. Fed broods were provided with dead laboratory mice every other day, averaging 100 g mice per day, as a simulation of the natural situation, in which the male deposits dead prey in the nest hole (Korpimäki 1987b; see Hörnfeldt *et al.* (2000) for further details on the feeding experiment). Broods that were abandoned by the parents before hatching was complete ($n = 10$), or in which more than one egg failed to hatch ($n = 7$), were not included in the experiment. As a result there were 11 fed and 13 control broods in 1998, and 17 fed and 26 control broods in 1999. Fed and control broods were evenly distributed in space and time, and within years did not significantly differ in laying date, clutch size, brood size (verified afterwards by *t*-tests) and hatching brood sex ratio (verified using generalized linear models with binomial errors). Nestling mortality within broods was analysed in generalized linear models, using binomial error distributions and logit link functions (Crawley

1993), using GLIM version 4.09. First, the effects of two potentially important covariates, laying date and brood size, were tested in log-likelihood ratio tests comparing the deviance of a model including the covariate being tested with a model excluding it. Significant covariates were kept in the model. The effects of supplemental feeding and year were then tested in a similar manner, by comparing the deviance of a model containing significant covariates and the factor to be tested with a model excluding the factor. The interaction between feeding treatment and year was tested by comparing the deviance of a full model with a model excluding the interaction term (Crawley 1993). Models were corrected for overdispersion, and their validity confirmed by visual inspection of residuals. Since mortality risk in owl nestlings increases with hatching sequence (Mikkola 1983), any mortality difference between the sexes could be due to an underlying sex bias in hatching sequence (e.g. Dijkstra, Daan & Buker 1990). Therefore median hatching sequence for males and females was compared, as was the sex ratio of last-hatched nestlings.

MOLECULAR SEXING

A 50- μ L blood sample was taken from each nestling by brachial vein puncture, 1–3 days after hatching. Samples were stored in SET buffer (in 1998) or Queen's buffer (in 1999). Sex determination of owl nestlings relied on polymerase chain reaction (PCR) amplification of one intron from the sex-chromosome linked *CHDI* gene, which in birds differs in size between the Z and W chromosomes (Fridolfsson & 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. For a more detailed description of the methods see Fridolfsson & Ellegren (1999).

NESTLING GROWTH

In 1998 only, nestlings were measured approximately every 2 days between hatching and fledging to obtain data on their growth patterns. Nestlings were weighed to the nearest g using a Pesola spring balance, and wing-length, measured from the carpal joint to the tip of the longest primary (after flattening and straightening the wing) was measured to the nearest mm using a stopped ruler. Measurements between hatching and fledging were obtained from 72 male nestlings (31 fed and 41 controls) and 38 female nestlings (18 fed and 20 controls) from 24 broods (11 fed and 13 controls). Nestlings that died before attaining asymptotic mass were excluded from the following analysis. A sigmoidal curve of the form $y = A/\{1 + \exp[-(x - x_0)/B]\}$ was used to describe mass (y) against age (x). A describes asymptotic mass and $0.25(A/B)$ was used to estimate the maximum rate of mass gain. Curves were fitted iteratively for each nestling using the Marquardt–

Levenberg algorithm in the program SigmaPlot version 5.0 (SPSS Inc. 1998), and in all cases the r^2 of curves exceeded 0.99. A straight line function, $y = y_0 + Ax$, was used to describe wing-length (y) against age (x), where A describes wing growth rate, 1–4 weeks after hatching (i.e. after the primary quills have emerged) and fitted using the same program. Effects of sex and supplemental feeding on mean curve parameters for nestlings in each brood were analysed using two-way analysis of variance (using type III sums of squares). Laying date and brood size were added to each model as covariates.

NATURAL FOOD SUPPLY

Indices of natural food supply for the owls were obtained from a running survey (within the Swedish National Environmental Monitoring Programme) of small mammals in which snap-trapping is carried out twice yearly, in spring (late May) and autumn (late September), in an area including the owl study site. Sampling was carried out in 58 regularly distributed 1-ha plots for three consecutive nights each season (see Hörnfeldt 1978, 1994 for details). The 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. To provide a measure of the change in food supply between trapping events, an index of rate of change in numbers in summer (from spring to autumn) and winter (from autumn to spring) was used. This was calculated according to the formula: $(N_t/N_{t-1})^{1/d}$, where N_{t-1} , N_t and d represent the consecutive trapping indices and the time lapse in days between them (see Hörnfeldt (1994) for details). When no voles were trapped, an index of 0.01 was used to avoid infinite rates of change. Differences in trapping indices for 1-ha plots between 1998 and 1999 were analysed using paired comparison t -tests.

Results

NESTLING GROWTH

Analysis of variance showed that female nestlings attained a higher asymptotic mass than males, that fed nestlings attained a higher asymptotic mass than controls, but that there was no significant interaction between sex and feeding treatment (Table 1). Of the covariates added to this model (i.e. laying date and brood size), only brood size was significant, having a negative effect ($\beta = -0.44$, $t_{34} = -2.64$, $P = 0.01$). Control females (mean \pm SE = 137.63 \pm 3.71 g) were 5% heavier than control males (130.81 \pm 2.12 g). Fed males (142.14 \pm 2.92 g) were 8% heavier than control males, while fed females (155.06 \pm 2.98 g) were 11% heavier than control females. Mass differences between the sexes emerged after approximately 2 weeks (halfway through the nestling period), and asymptotic

Table 1. Results of two-way analysis of variance of the effects of sex and supplemental feeding on mean growth parameters in broods of Tengmalm's owl nestlings

	<i>F</i>	d.f.	<i>P</i>
Asymptotic mass			
sex	4.74	1, 34	0.04
feeding	14.69	1, 34	<0.001
sex × feeding	0.34	1, 34	0.56
Max. rate of mass gain			
sex	2.03	1, 34	0.16
feeding	1.51	1, 34	0.23
sex × feeding	0.01	1, 34	0.92
Wing growth rate			
sex	0.03	1, 34	0.85
feeding	0.44	1, 34	0.51
sex × feeding	0.55	1, 34	0.46

Table 2. Results of log-likelihood ratio tests (LLR) of the effects of supplemental feeding and year on Tengmalm's owl nestling mortality. *N* = no. of broods

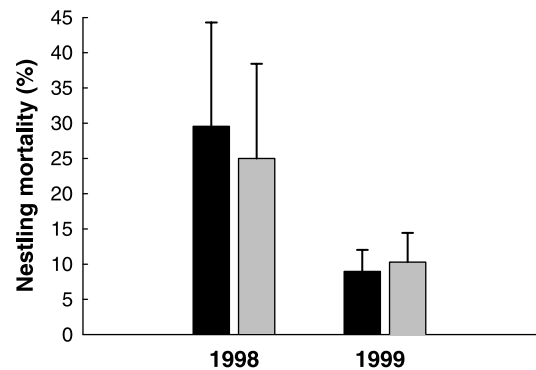
	<i>N</i>	LLR	d.f.	<i>P</i>
Overall mortality	67			
feeding		0.39	1	0.53
year		1.44	1	0.23
feeding × year		3.96	1	0.05
Female mortality	65			
feeding		0.01	1	0.75
year		0.80	1	0.37
feeding × year		0.01	1	0.94
Male mortality	64			
feeding		0.58	1	0.45
year		0.89	1	0.34
feeding × year		7.55	1	0.01

mass was attained after approximately 3 weeks. Neither maximum rate of mass gain nor rate of wing growth differed between the sexes, and there was no effect of feeding (Table 1). Neither of the covariates (i.e. laying date and brood size) had any significant effect on maximum rate of mass gain or wing growth.

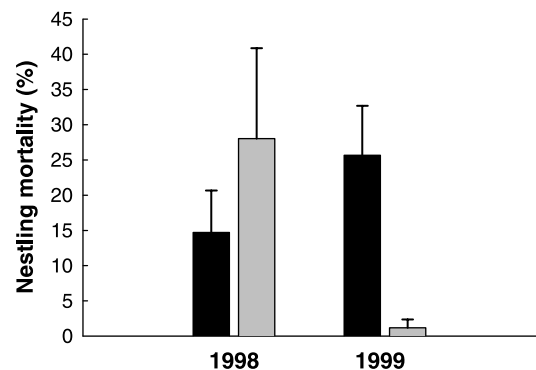
NESTLING MORTALITY

For both sexes combined, neither supplemental feeding nor year had any independent effect on nestling mortality, although the interaction between feeding treatment and year was significant (Table 2). Supplemental feeding significantly decreased nestling mortality in 1999 only (planned post hoc contrast: $\chi^2_1 = 4.03$, $P = 0.04$). For female nestlings, neither feeding treatment nor year had any significant effect, and there was no significant interaction (Table 2, Fig. 1a). However, for male nestlings, while the main terms were not significant, the interaction between feeding treatment and year was significant, with feeding decreasing mortality in 1999 only ($\chi^2_1 = 7.63$, $P = 0.01$; Table 2, Fig. 1b). Of the

(a) Females



(b) Males

**Fig. 1.** Mean (a) female mortality and (b) male mortality (%) in control (black bars) and fed (grey bars) broods of Tengmalm's owl nestlings in 1998 and 1999. Note that the natural food supply was more favourable in 1998. Error bars represent +1 SE.

covariates tested (i.e. laying date and brood size), laying date was consistently significant, with mortality increasing with increasing laying date, while brood size had no significant effect. Mortality was mostly confined to the youngest nestlings (71% of the 55 nestlings that died before fledging), a pattern that was similar for both sexes and years. Median hatching sequence did not differ between the sexes in 1998 ($U = 2078.0$, $n = 138$, $P = 0.79$) or 1999 ($U = 6005.5$, $n = 231$, $P = 0.19$). Sex ratio of last-hatched nestlings was male-biased in 1998, though not significantly so (63% male; $\chi^2_1 = 1.04$, $P = 0.31$), and reflected the overall male-biased sex ratio in this year (Hörnfeldt *et al.* 2000). Likewise, there was no significant sex-bias in last-hatched nestlings in 1999 (53% male; $\chi^2_1 = 0.01$, $P = 0.99$).

NATURAL FOOD SUPPLY

While vole density in spring did not significantly differ between 1998 and 1999, vole abundance in autumn was higher in 1998 than 1999, and thus the former year was characterized by a greater increase in vole abundance during summer (Table 3). In addition, the winter decline in vole abundance was lower during 1997/98 than 1998/99 (Table 3).

Table 3. Mean vole trapping indices (n per 100 trap-nights) for 58 1-ha plots in spring and autumn, and derived rate of change in vole numbers per day during the previous winter and current summer in 1998 and 1999

Vole supply parameter	1998	1999	Paired t (P)
Trapping index			
spring	1.39	1.33	0.25 (0.81)
autumn	9.68	3.07	10.03 (0.01)
Rate of change day ⁻¹			
previous winter	0.999	0.986	7.34 (0.01)
summer	1.025	1.012	3.24 (0.01)

Discussion

The two years during which the feeding experiment was carried out were characterized by different phases of the vole population cycle. During 1998, vole numbers increased substantially between spring and autumn, after having declined slightly during the previous winter. Thus the owls experienced a relatively stable food supply before breeding (i.e. late winter–early spring), which then increased throughout the summer. Supplemental feeding had no effect on nestling mortality during 1998 (Table 2; see also Hörnfeldt *et al.* 2000), since the control broods probably also experienced a good food supply. Food provision experiments do not usually raise production to levels exceeding those recorded during especially favourable natural conditions (Boutin 1990; Newton 1998), and supplemental feeding does not necessarily eliminate sibling aggression in facultatively siblicidal birds (Mock 1985; Mock, Lamey & Ploger 1987), so the youngest nestlings might still have died despite the plentiful food supply. In 1999, voles had declined markedly during the previous winter and only increased slightly during summer. In addition, owl breeding density was higher than in 1998 (nestbox occupancy being 15% and 22% in 1998 and 1999, respectively), probably increasing competition for food. Thus while spring vole abundance was similar during the two years, owls breeding in 1999 experienced a more meagre food supply throughout the season compared with those in 1998. Under these conditions supplemental feeding significantly reduced nestling mortality (Table 2).

In Tengmalm's owl, a degree of sexual size dimorphism is apparent after halfway through the nestling stage. In control nestlings, females were 5% heavier than males, which is a difference similar to that observed in adults in autumn (Hipkiss 2002). Although the larger sex in size-dimorphic birds usually attains mass at a higher rate than the smaller one (Teather & Weatherhead 1994), we found no evidence of this. However, a more sensitive investigation of growth rate might have revealed such a difference. Despite adult female Tengmalm's owls having slightly longer wings than males, no sex difference in wing growth rate was detected in nestlings. Juvenile females probably require more time to fully develop their wings than males (cf. Teather & Weatherhead 1994),

although this difference would only be noticeable after the young leave the nest. Nestlings of both sexes provided with supplemental food attained a higher mass at fledging than controls, analogous to the difference in asymptotic mass recorded in years of differing food supply (Carlsson & Hörnfeldt 1994). It is conceivable that supplementary-fed nestlings might enjoy higher survival after fledging, particularly when they begin to fend for themselves. That supplemental feeding might have benefited nestlings that survived to fledging, but did not reduce the low level of mortality in 1998 further suggests that supplemental feeding does not completely reduce sibling aggression (cf. Mock 1985; Mock *et al.* 1987).

Given that female Tengmalm's owl nestlings are larger than males, they might be expected to suffer from higher mortality than males when food supply is limited (Clutton-Brock *et al.* 1985; Weatherhead & Teather 1991). Consequently, we expected female nestling mortality to be lower in supplementary-fed broods than in control broods. In 1998, natural conditions seemed too favourable for differential mortality to occur, and there was probably too little contrast between fed and control broods for supplemental feeding to have any effect on nestling mortality (Hörnfeldt *et al.* 2000). In 1999, conditions were less favourable, and supplemental feeding reduced overall nestling mortality. However, contrary to expectation, female mortality was not lower in supplementary-fed broods (Fig. 1a). This suggests that in Tengmalm's owls, female nestlings do not suffer increased mortality in unfavourable conditions as a consequence of their larger size. In contrast, male mortality was significantly lower in supplementary-fed broods than in control broods (Fig. 1b), suggesting that in control broods, males, rather than females, were placed at a disadvantage and did not receive enough food. In captive American kestrels *Falco sparverius*, Anderson *et al.* (1993a) observed that the larger female nestlings completely dominated their male siblings when prey items were small enough to be monopolized by one nestling, and they also dominated when items were of medium size but too large to be monopolized. Only for very large prey items was competitive advantage equal between the sexes (see also Mock 1985). Thus, despite females being larger than males (to a similar degree as in Tengmalm's owl) and requiring more food during growth (Anderson *et al.* 1993b), their large size provided an advantage in interference competition for food items. Admittedly, unlike Anderson *et al.* (1993a), we were unable to directly observe nestling interaction. However, Anderson *et al.* (1993a) stated that dominance of the larger sex could be expected in sexually size-dimorphic semi-altricial nestlings (*sensu* Ricklefs 1972), which have well-developed motor functions, and are able to physically compete with their nest-mates. Tengmalm's owl certainly fits this definition, and voles, the natural food of Tengmalm's owl, and the mice provided as supplemental food, fit the category of medium-sized

prey items (*sensu* Anderson *et al.* 1993b) that female nestlings might not be able to monopolize but could probably control and consume a larger share of. When food is limited, as it probably was in control broods in 1999, some male nestlings might not be able to obtain enough food to survive. However, supplemental feeding in 1999 at least partly alleviated the males' disadvantage, although as previously mentioned, sibling aggression was probably not eliminated completely (cf. Mock 1985; Mock *et al.* 1987). In birds with asynchronously hatching broods, the age hierarchy in itself often has most influence over dominance and nestling mortality (Bortolotti 1986; Slagsvold 1990; Drummond *et al.* 1991). In Tengmalm's owl, dominance of the larger sex probably works in concert with the age hierarchy within the brood, since mainly only the youngest nestlings are affected by this phenomenon. It was therefore important to check that there was no underlying sex bias in the hatching sequence within broods, since if males tended to hatch last, and were therefore more often the youngest brood members, then this alone would have explained why supplemental feeding reduced mortality of males only. This was not the case, and therefore male-biased mortality *per se*, probably owing to female dominance, could plausibly explain the counteractive effect of supplemental feeding on male mortality.

In conclusion, although Tengmalm's owls are moderately sexually size-dimorphic, the larger female nestlings did not appear to be at a disadvantage, even when food supply was relatively low. On the contrary, it seemed as though their large size enables them to out-compete their smaller male siblings, and leads to increased male mortality when food is limited. This might be a general pattern in moderately sexually size-dimorphic birds (Lessells 2002), and is likely to be the case in most owl species, which show moderate sexual size dimorphism and often consume small partially monopolizable mammalian prey. This study also highlights the importance of measuring natural food supply when carrying out food supplementation experiments, and of repeating them over more than one season, to ensure that supplemental feeding fulfils its purpose. The high-amplitude vole population cycles of northern Sweden, with which Tengmalm's owl's breeding biology is intertwined, enabled this point to be clearly illustrated.

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