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Size-mediated dominance and begging behaviour in Eurasian kestrel broods

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ABSTRACT

Resource allocation from parents to their offspring can be modulated by inter-sexual size dimorphism. High dimorphism promotes differential costs in rearing male and female offspring and unequal competitive ability among siblings. We examined whether any of these types of biases occur in Eurasian kestrels, *Falco tinnunculus*, in which females are larger than males. We measured begging behaviour of nestlings during the second week after hatching to establish how parents respond to begging signals. In addition, we looked for possible costs of begging as a trading function with T-cell-mediated immune response or growth. Begging display was higher in nests suffering from food shortage. Parents (mothers in 98% of the cases) allocated more food to chicks begging more intensely. Female chicks obtained more food from parents than males, but only in nests in which parents provided the chicks with prey items small enough to be swallowed whole (without dismembering) by the chicks. No difference in begging calls was observed between male and female nestlings. However, female chicks were closer to the parent in non-dismembering nests. Begging display was not associated with T-cell-mediated immunity or growth. Our results show a clear response of food provisioning by parents to begging display of nestlings, and suggest that the advantage of female nestlings in food acquisition was due to their competitive superiority over male sibling nest-mates in scramble competition for monopolizeable prey.

Keywords: begging, *Falco tinnunculus*, food provisioning, immune response, raptor, sex allocation, sexual size dimorphism, sibling competition.

INTRODUCTION

Fisher (1930) suggested that when the reproductive value of sons and daughters is similar, equal parental expenditure on the sexes should promote an offspring sex ratio biased towards the sex with lower per capita cost to parents. Therefore, in sexually size-dimorphic species, one should find biased sex ratios at the end of parental investment towards the less

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costly (smaller) sex (Komdeur and Pen, 2002). However, the reproductive values of the two sexes are not necessarily equal (Trivers and Willard, 1973; Charnov, 1982), and sex-biased provisioning has been detected when sons and daughters differed in their energy requirements (see Clutton-Brock, 1991, for a review). Furthermore, Lack (1954) suggested that in sexually size-dimorphic birds, the nestlings of the larger sex can survive better because of a competitive advantage in sibling competition. This prediction has been corroborated (Anderson *et al.*, 1993; Oddie, 2000). One might therefore expect that nestlings of the larger sex would be less likely to starve when food becomes scarce, resulting in a biased sex ratio in favour of the larger sex (Anderson *et al.*, 1993). One way of exploring these ideas is to study the food allocation of parents in relation to offspring sex, and sex- and size-related resource allocation to different behavioural (e.g. begging) and physiological (e.g. immunity) functions in the offspring.

It is unclear whether there are sex-related differences in begging behaviour, growth or physiology, or what the possible cues are that parent birds could use for sex discrimination (see Lessells, 2002). Begging behaviour is expected to be energetically costly, as this display involves not only vocalizations, but also a physical effort through sibling competition for better positions with respect to the parents (e.g. Anderson *et al.*, 1993; Leonard *et al.*, 2000). Recent studies have suggested a trade-off between begging and growth, apparently supporting the idea of honest signalling (Kilner, 2001; Rodríguez-Gironés *et al.*, 2001). As the maintenance of immune function against parasites and pathogens is energetically and nutritionally costly (Lochmiller and Deerenberg, 2000), there might also be a trade-off between investment in immune function, begging behaviour or growth (Saino *et al.*, 1997; Hõrak *et al.*, 1999).

In a previous study, we detected sex-related differences in one component of the immune function in sexually size-dimorphic Eurasian kestrels, *Falco tinnunculus* (Fargallo *et al.*, 2002). These differences could generate sex-biased nestling survival. In this paper, we explore the potential sex-related relationships among begging behaviour, immune function and growth, and the role of parents as possible mediators in these relationships in kestrels. First, we studied how parents and/or sex-related sibling competition mediate food allocation to male and female offspring by assessing parental responses to chick begging signals. Second, we examined potential trade-offs between begging display and growth or cell-mediated immune response. Finally, we assessed whether female kestrel nestlings have better access to food than their male siblings when parents provision the nests with (small) alternative prey types in the wild, as has been suggested for all raptor species (Anderson *et al.*, 1993).

METHODS

Study area, study species and video-recording

We studied kestrels during the breeding seasons of 1998 and 1999 in the Kauhava region, western Finland (63°N, 23°E), where kestrels breed in nest boxes mounted on the gables of barns (Korpimäki and Wiehn, 1998). During these years, the densities of voles, the main prey of kestrels (Korpimäki, 1985, 1986), were markedly lower in 1998 than in 1999 (see Fig. 1 in Korpimäki *et al.*, 2002). The Eurasian kestrel is a sexually size-dimorphic species, with females being 20% heavier than males (Massemin *et al.*, 2000). During the first 2 weeks of life of the nestlings, male parents deliver prey items to the female parents, who then

divide the prey among the chicks. After 2 weeks, parents bring prey items to the nest and leave them for the chicks to dismember and eat by themselves. Nests were visited to estimate hatching asynchrony. We scored the nestlings as first-, intermediate- and last-hatched. To better evaluate parental decisions for food provisioning to one or the other sex, we conducted our study during the first half of the nestling period (at the end of the second week after hatching).

We studied 29 broods (9 in 1998 and 20 in 1999). Broods were video-recorded continuously for 24 h (see Wiehn *et al.*, 2000, for detailed camera installation procedures). We were able to film on average 13 complete feeding sessions (range 3–25) per nest. Video-taping took place when the within-brood age of the chicks was 11.0 ± 0.2 days (mean ± standard deviation, $n = 140$). At the time when we installed the camera, we weighed and individually marked each chick on the head with colour felt-pens. Mass, tarsus and wing lengths of fledglings were measured 23–27 days after hatching.

Amount of food consumed

In each feeding session, we recorded the identity of the parent (female or male), the prey species, the number of pieces into which the prey was divided and the number received by each nestling. The amount of food that each chick consumed in each feeding season was defined as the number of pieces they received. To compare the amount of food consumed by nestlings between dismembered and non-dismembered prey items, we estimated the mean weight of a piece of food. We divided the mean weight of prey items (data from Norrdahl and Korpimäki, 2002) consumed by kestrels by the mean number of pieces in which the prey was divided. We recorded a mean value of 0.64 g for the bank vole, *Clethrionomys glareolus* (18 g/mean = 28.0 ± 8.7, $n = 13$); 0.59 g for *Microtus* spp. (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*: 24 g/mean = 41.1 ± 18.2, $n = 35$); 0.48 g for the house mouse, *Mus musculus* (15 g/mean = 31.0 ± 8.2, $n = 29$); and 0.51 g for the common shrew, *Sorex araneus* (9 g/mean = 17.7 ± 9.7, $n = 11$). The mean value for a piece of food was 0.55 g. When a partial prey was eaten without division, we visually estimated the portion consumed using the following estimation: 3/4 prey without head, 2/4 prey without head and without superior extremities, 1/4 prey only with tail and inferior extremities. We estimated the number of pieces corresponding to the partial prey items by using the following formula: number of pieces = portion consumed × mean weight of the prey/0.55. For common lizards, *Lacerta vivipara*, we assigned the mean body mass (3 g) obtained from the literature (van Damme *et al.*, 1991) corresponding to 5.5 pieces of food. In the case of insects (only occasionally found items), we assigned the value of one piece for each insect item. Chicks never swallowed water voles (*Arvicola terrestris*) or avian prey items with no previous dismembering by parents.

Dismembering versus non-dismembering nests

We considered a high presence of insects, lizards and shrews in the diet to be indicative of environmental food restrictions (Korpimäki, 1985, 1986; see above). As expected, nestlings were fed with a higher frequency of lizards and shrews in the year of low food supply (1998) (Yates corrected chi-squared: $\chi^2_1 = 75.18$, $P < 0.0001$ and $\chi^2_1 = 9.88$, $P = 0.002$, respectively) than in a year of high food supply (1999). Insect prey was found in only two nests, for which

we eluded to make statistical comparisons. In five nests (four in 1998 and one in 1999), parents did not dismember the prey because the whole prey items were small enough to be swallowed whole by the nestlings. In these nests, the presence of lizards and shrews in the nestling diet was significantly higher than in the rest of the nests (Yates corrected chi-squared: $\chi^2_1 = 8.67$, $P < 0.003$ and $\chi^2_1 = 4.68$, $P = 0.031$, respectively). Parents from non-dismembering nests fed their chicks with significantly less voles (the field vole, the sibling vole, the bank vole and the water vole) than those from dismembering nests (Yates corrected chi-squared: $\chi^2_1 = 8.32$, $P = 0.004$). Based on these prey-size characteristics, we divided the nests into 'dismembering' and 'non-dismembering' nests.

Begging behaviour

We defined several variables in relation to the observed begging display of nestlings. Begging variables were always estimated as the mean value for all filmed feeding sessions in each nestling. First, begging persistence was defined as the proportion of time the chick was calling for food throughout one feeding session. This variable was closely correlated with the length of the feeding session, begging calls being less persistent in longer feeding sessions ($r = -0.65$, $F_{1,138} = 98.44$, $P < 0.001$). We used the residuals from this regression as an estimate for begging persistence. Second, begging frequency was defined as the proportion of feeding sessions in which the chick begged. Third, we defined the nest position of the chick as the proximity of a given chick to the parents in relation to the remaining chicks. To allow a comparison among different brood sizes (from three to seven chicks), we assigned proximity values of 1 (the closest chick), 2 (the ones in between) and 3 (the farthest one). Begging persistence, begging frequency and nest position can be considered different behavioural aspects conforming to the begging display performed by the nestlings (e.g. Price and Ydenberg, 1995). We performed a principal component (PC) analysis by combining these three begging variables. Only one component was extracted explaining 80.1% of the variation in these variables (eigenvalue = 2.41). Individuals begging more persistently during the feeding session also begged in more feeding sessions and were closer to the mothers. We used PC1 as the combining variable describing the conspicuousness of begging display for each chick.

Immunity assessment

We measured T-cell-mediated immunity of chicks in 1999. We used a skin test that measures the proliferative response of circulating T-lymphocytes to phytohaemagglutinin-P (PHA). PHA is a mitogen commonly used in studies of birds because it is considered a benign (Merino *et al.*, 1999) and useful method to evaluate thymus-dependent function (Goto *et al.*, 1978). Kestrel chicks were injected intradermically in the wing web with 0.3 mg of PHA dissolved in 0.1 ml of phosphate-buffered saline. The thickness of wing webs was measured three times with a sliding calliper (to the nearest 0.05 mm) at the injection site before (24–27 days after hatching) and 24 h after injection, these three measurements being repeatable (Fargallo *et al.*, 2002). We used the mean value of these three measurements for statistical analyses. The difference between initial wing web thickness and swelling is used as a response estimate (Smits *et al.*, 1999).

The statistical procedures are given in the Appendix.

RESULTS

Mothers fed the chicks in 98% of cases ($n = 388$). At the time of filming (mean brood age 11 days), only sex of chicks and study year were found to explain some of the variation in body mass. Female nestlings were marginally heavier than males (males: 149.8 ± 5.0 g; females: 155.4 ± 4.9 g; GLMM: $F_{1,109} = 3.53$, $P = 0.063$). Eleven-day-old nestlings were lighter in 1998 than in 1999 (1998: 146.4 ± 6.4 g; 1999: 158.9 ± 4.6 g; GLMM: $F_{1,109} = 4.53$, $P = 0.036$).

Chicks received on average fewer pieces of food from their parents in 1998 (2.2 ± 1.8) than in 1999 (6.9 ± 1.6) (Table 1). Female nestlings received more food from their parents, but only in nests in which parents did not dismember food items to their offspring; no difference was observed in nests in which parents dismembered food items (Table 1; Fig. 1a). Chicks exhibiting a more conspicuous begging display also received more food (Table 1).

Chicks from non-dismembering nests begged more than those from dismembering nests (GLMM: $F_{1,108} = 7.90$, $P = 0.006$). Female nestlings tended to perform a more conspicuous begging display than males, but only in non-dismembering nests (GLMM: interaction sex × dismembering, $F_{2,108} = 3.05$, $P = 0.084$). As female nestlings from non-dismembering nests received significantly more food than males, we explored separately the interaction between sex of chicks, study year and prey-dismembering for each measured begging variable to determine which behaviour was responsible for this difference. There was no inter-sexual difference in begging persistence or begging frequency (GLMM: both $P > 0.4$). However, female nestlings were significantly closer to the mother (nest position of the chick) in nests without than with dismembered food items (GLMM: interaction, $F_{2,109} = 7.66$, $P = 0.007$; Fig. 1b). Chicks begged in more feeding sessions in 1998 than in 1999 (GLMM: $F_{1,111} = 9.89$, $P = 0.002$), but not more persistently (GLMM: $F_{1,111} = 0.95$, $P = 0.33$).

Controlling for the effect of sex, chicks of dismembering nests had a higher body mass at fledging than chicks of non-dismembering nests (Table 2; Fig. 1c). The significant interaction was due to an inter-sexual difference in the body mass of chicks, which was higher in dismembering than non-dismembering nests. Nestlings that had a higher body mass and received more pieces of food at the age of 11 days also attained a higher body mass 2 weeks later at fledging (Table 2).

To analyse the T-cell-mediated immunity (CMI) response of chicks, which was measured only in 1999, we excluded the term dismembering from the model because there was only one non-dismembering nest. As we have found previously (Fargallo *et al.*, 2002), the CMI response was affected by sex (GLMM: $F_{1,82} = 4.01$, $P = 0.049$) and body mass at fledging (GLMM: $F_{1,82} = 10.32$, $P = 0.002$) but not by any of the other variables measured.

Table 1. Results of the mixed model examining factors affecting the amount of food consumed by kestrel nestlings at the age of 11 days

Source	d.f.	Estimate	*F*	*P*
Sex	1,108	3.951	9.72	0.002
Study year	1,108	4.844	7.53	0.007
Sex × dismembering	2,108	3.261	4.03	0.020
Begging	1,108	1.496	26.51	0.000

Note: Only significant variables are presented.

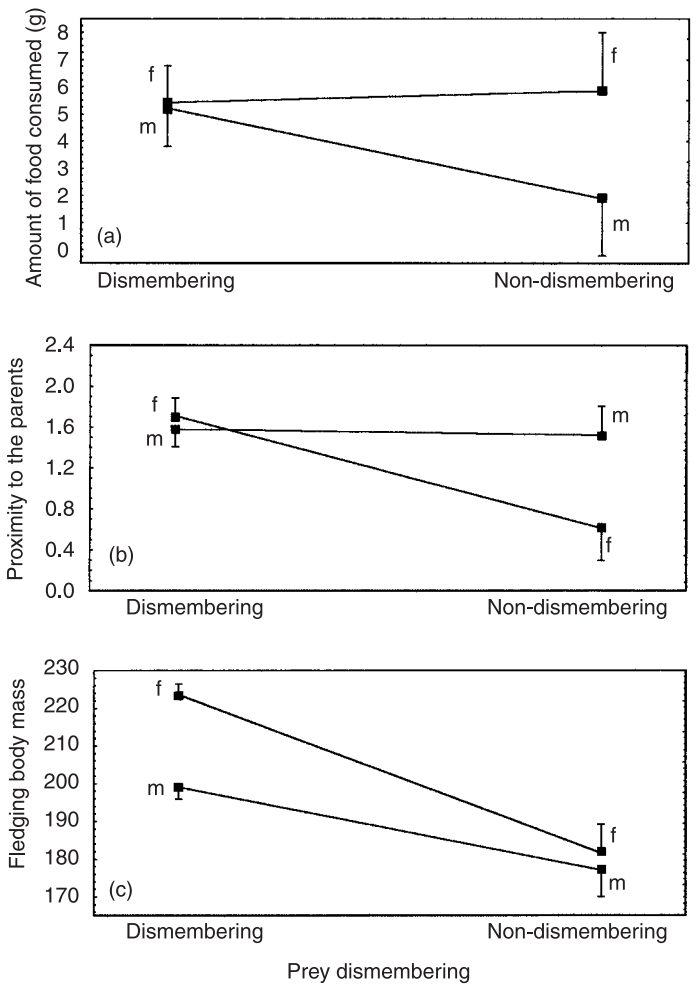

Fig. 1. Differences in the amount of food consumed (a), proximity to the parents (b) and body mass (c) between male (m) and female (f) kestrel nestlings with respect to prey dismembering by parents. Mid-whiskers show standard error.

Table 2. Results of the mixed model examining different factors affecting fledging body mass of kestrels

Source	d.f.	Estimate	*F*	*P*
Sex	1,107	4.779	20.07	0.000
Dismembering	1,107	41.399	16.20	0.000
Sex × dismembering	2,107	19.769	9.69	0.002
Body mass (11 days)	1,107	0.179	20.02	0.000
Food consumed	1,107	0.629	4.75	0.031

Note: Food consumed was defined as the number of pieces of food consumed by chicks (see Methods).

DISCUSSION

The nestlings that begged more intensely and in more feeding sessions reached a better position in relation to the providing parent and were provided with a greater amount of food. Chicks in nests in which the parents did not divide prey items begged more, but reached the fledging stage with a lower body mass than those in nests with parental prey division. This suggests that chicks in non-dismembering nests suffered from a food shortage and that there is a close connection between hunger and begging. As mothers fed more those chicks that begged more, we suggest that mother kestrels may interpret the begging behaviour of chicks as a signal for hunger.

Our results appear to indicate that feeding behaviour of female kestrel parents was not selectively varied in relation to the sex of offspring even at different levels of food resources. However, we cannot say whether a provisioning bias to daughters in non-dismembering nests is due to female advantage in sibling competition or maternal preference when food is restricted. This latter idea is not in accordance with previous studies in our kestrel population, however, where pairs breeding in years of low food supply and females with a poorer body condition tended to produce male-biased fledging sex ratios (Korpimäki *et al.*, 2000). Further experimental work in this respect is required.

The extent of sexual dimorphism in body mass of chicks was not yet very distinct in the phase of the nestling period when prey division was monitored (females were on average 5.6 g, or 3.6%, heavier than males). However, this difference in size was enough for females to reach better positions inside the nest to obtain food. Female kestrel nestlings, therefore, seem to have competitive superiority over their male nest-mates in access to food when the food item is small and monopolizeable, which has also been reported in American kestrels (Anderson *et al.*, 1993). That female nestlings did not use their competitive superiority to obtain more food from parents in dismembering nests could be due to the between-group difference in food resources. Parents in non-dismembering nests provided the chicks mainly with small, alternative prey items, such as lizards and shrews, while voles, in particular *Microtus* spp., were more often delivered by parents in dismembering nests. The dismembering nests apparently suffered less from food restrictions because parents provided enough food to cover the nutritional demands of chicks, potentially decreasing sibling competition.

In our study area and elsewhere in northern Europe, the abundance of voles fluctuates in a cyclic manner in periods of 3–4 years (e.g. Korpimäki and Wiehn, 1998; Korpimäki *et al.*, 2002). It is mainly in years of low vole abundance, such as 1998, when kestrels feed on alternative prey types (e.g. lizards and shrews; Korpimäki, 1985, 1986). Female size-dominance in sibling competition may, therefore, only have an impact every third or fourth year in our study population, but it may be of more importance in more southern kestrel populations, where the food of kestrels consists of proportionally more small prey items (Gil-Delgado *et al.*, 1995; Aparicio, 2000). On this scenario, it would be expected that more female than male chicks survive during the chick-rearing phase in nests or years of low food supply, resulting in a skewed fledging sex ratio towards females.

The cell-mediated immune response was lower in male than female nestlings. This finding is to be expected, considering the observed superiority of female offspring in sibling competition. This female advantage could be maintained or even increased after the age of 11 days until fledging, because during that period mothers do not dismember the prey delivered and the sexual size dimorphism of chicks is more accentuated. However, after removing the effect of body mass we still observed an inter-sexual difference in immune

response, but found no trade-off between begging display and immune response (in 1999) or begging display and body mass (both in 1998 and 1999). Thus, we cannot say whether the sexual difference in immune response is a direct consequence of sexual variation in begging effort or scramble competition. Other physiological mechanisms, perhaps induced by sibling competition, might mediate immune function in male nestlings, especially when food becomes scarce (Fargallo *et al.*, 2002).

In conclusion, we have shown for a non-passerine species of bird a clear correlation between the begging display of chicks and the food provisioning of parents. We suggest that the begging display of kestrel chicks might be interpreted as an honest advertisement of need, and that kestrel parents respond to this signal by distributing the food to the chicks with a more conspicuous begging display. However, experimental studies are required to verify this. Our results also suggest that the feeding behaviour or food distribution of parents, or at least mothers, was not associated with offspring sex. It is likely that the differential food intake of female and male chicks in nests in which they were able to eat the prey by themselves can be attributed to female nestling superiority in scramble competition. On the other hand, we cannot exclude the idea of a preferential food allocation of parents to female nestlings when food is in short supply. Finally, we found that begging effort was not reflected in the components of avian immune function or in body mass at the end of the nestling period, suggesting that the begging variables we measured are not traded off with the T-cell-mediated immune response or growth. More studies of inter-sexual physiological and behavioural differences are required to predict fledging sex ratios or nestling sex-related mortality through classical sex allocation theory.

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APPENDIX: STATISTICAL PROCEDURES

Our data were unbalanced and unsuitable for conventional analysis of variance. We therefore analysed the data incorporating random and fixed effects using general linear mixed models (PROC MIXED) in Randomized Complete Block Designs (Littell *et al.*, 1996) in SAS statistical software (SAS Institute, Cary, NC, USA). We performed five models using the following response variables: (1) body mass of nestlings at the time of video recording (11 days old); (2) begging display (PC1); (3) amount of food consumed; (4) body mass of nestlings at the end of nestling period (mean = 24.4 ± 1.7 g, $n = 140$); and (5) T-cell-mediated immunity response. As possible explanatory variables we considered: (1) laying date, (2) brood size, (3) body mass at the time of recording, (4) body mass at fledging, (5) age of chicks, (6) brood sex ratio, (7) position of the chick in the hatching sequence, (8) sex, (9) year and (10) prey-dismembering (dismembering *vs* non-dismembering nests). We considered that chicks from the same nest were not independent samples. Therefore, nests were treated as random effects using a randomized complete block design, in which variation in each chick variable was controlled for nest and the remaining explanatory variables. Year, sex, prey-dismembering and position in the hatching sequence were included in the model as fixed factors. By doing so, we controlled for individual traits in analyses while avoiding pseudo-replication.

A clutch-size manipulation was performed in 1999 in our study population (Fargallo *et al.*, 2002). To increase the sample size in the present study, we included those nine experimental nests. We statistically removed the effect of experimental treatment by including it in the random structure of models. Some of the explanatory variables could covary, thus we fitted their effects to the observed data following a forward stepwise procedure, testing the significance of each variable one by one, and adding only the variable that resulted in the largest increase in the fit to the model. All tests were two-tailed.