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Sex-specific nestling body mass in relation to brood sex composition in the Eurasian Sparrowhawk *Accipiter nisus*

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Vedder O., Dijkstra C., Dekker A.L., Waasdorp S. & Visser G.H. 2005. Sex-specific nestling body mass in relation to brood sex composition in the Eurasian Sparrowhawk *Accipiter nisus*. *Ardea* 93(2): 179–187.



The trade-off between brood size and offspring quality, as predicted by life history theory, has been extensively studied in birds. However, in sexually size-dimorphic birds, where the larger sex requires more investment from the parents, the potential additional trade-off between brood sex ratio and offspring quality has received less attention. Effects of brood sex composition on nestling fitness can have implications for optimal sex allocation strategies. A harmful effect of a higher proportion of the larger sex on either one of the sexes predicts selection towards parents producing the less harmful, smaller sex. In addition to Fisherian equal allocation this should lead to considerable sex ratio biases in extremely sexually size-dimorphic birds. We tested this in the Eurasian Sparrowhawk *Accipiter nisus*, where female nestlings require about 40% more parental investment than male nestlings. Sex-specific nestling body mass, calculated as the relative difference with the average body mass, corrected for age, for both sexes, was used as an indicator of nestling quality. With a sample size of 120 broods, containing 483 nestlings, we found that individual nestlings were of lower body mass when they hatched in larger and female dominated broods. This effect was particularly pronounced in female nestlings. Under these conditions, sex ratio theory predicts a male bias in the population. However, this is not supported by empirical evidence from literature.

Key words: Sexual size dimorphism, sibling competition, parental investment, sex allocation, Eurasian Sparrowhawk, *Accipiter nisus*

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INTRODUCTION

Sex allocation theory predicts that natural selection favours equal parental investment in both sexes of offspring, at the population level (Fisher 1930), and that individual parents should adjust the sex ratio of their offspring to prevailing envi-

ronmental conditions, in order to maximize inclusive fitness (Trivers & Willard 1973, Frank 1990). Although predictions of sex allocation theory are empirically supported in some taxa, most notably haplodiploid parasitoids (Godfray 1994, Herre *et al.* 2001), empirical data fit less well to theory in vertebrates exhibiting chromosomal sex determi-

nation (Cockburn *et al.* 2002, Krackow 2002, West *et al.* 2002). The reason for a poor fit in vertebrates may be a limited control of parents over offspring sex (Krackow 2002, Pike & Petrie 2003), or simplistic assumptions regarding vertebrate life histories (Pen & Weissing 2002).

Whether facultative adjustment of brood sex ratio is a general phenomenon in birds is still subject to discussion, with recent meta-analyses drawing opposing conclusions (West & Sheldon 2002, Ewen *et al.* 2004). Unfortunately, no proximate mechanism has yet been identified that enables parents to control offspring sex in birds (Pike & Petrie 2003, but see Pike 2005). However, extreme examples of sex ratio biases, as found in Seychelles Warblers *Acrocephalus sechellensis* (Komdeur *et al.* 1997, 2002), Eclectus Parrots *Eclectus roratus* (Heinsohn *et al.* 1997) and Domestic Pigeons *Columba livia* (Pike 2005), do suggest mechanisms to control offspring sex to occur in at least some bird species.

Since birds are iteroparous, life history theory predicts that the amount of energy parents spend on a brood is traded off against their future reproductive success. Therefore, when brood size is experimentally increased, parental effort should not necessarily increase proportionally with the increased demand of the brood. For nestlings in experimentally enlarged broods, this can lead to reduced growth (Smith *et al.* 1989, Dijkstra *et al.* 1990, Robinson & Rottenberry 1991), higher mortality (Tinbergen 1987, Dijkstra *et al.* 1990, Tinbergen & Boerlijst 1990, de Kogel 1997) and a lower chance to be recruited as a breeder in the following year (Gustafsson & Sutherland 1988, Tinbergen & Daan 1990). Since in general more young fledge from larger broods, parents should also trade off offspring number against reduced offspring growth, when applying the optimal level of investment (reviewed by Dijkstra *et al.* 1990, Stearns 1992).

In sexually size-dimorphic species there often is a difference in requirements (i.e., the amount of parental investment needed to achieve a given fitness) between both sexes of offspring (Anderson *et al.* 1993, Krijgsveld *et al.* 1998, Riedstra *et al.* 1998,

Magrath *et al.* 2004, Vedder *et al.* 2005). This gives potential for an additional trade-off between offspring quality or number and the sex ratio of a brood, since a brood with a greater proportion of the more expensive sex has a higher demand for food (Dijkstra *et al.* 1998). Empirical results indeed show that individual offspring are of lower quality, in terms of body condition, when a brood contains a higher proportion of the more expensive sex (Nager *et al.* 2000, Laaksonen *et al.* 2004).

It is likely that, when the sexes compete for food provisioned by the parents, the possible competitive advantage of larger size does not relate proportionally to the disadvantage of greater requirement. Either the smaller sex or the larger sex would then be more vulnerable to increased competition by a high food demand of the brood (i.e., a large brood size and/or a high proportion of the expensive sex). Competitive advantages of the smaller and the larger sex have both been documented (reviewed by Råberg *et al.* 2005). Given a certain brood size, this may result in two possible scenarios: 1) the smaller sex is negatively affected by a greater proportion of siblings of the opposite sex, or 2) the larger sex is negatively affected by a greater proportion of siblings of the same sex. When, as in the first scenario, one sex is more likely to be negatively affected by siblings of the opposite sex, theory predicts a sex ratio adjustment towards the most vulnerable sex (Uller 2003, in press). Alternatively, when, as in the second scenario, one sex is negatively affected by having same sex siblings, theory predicts an adjustment towards the less vulnerable sex (Uller 2003, in press). Hence, when in both scenarios it is the presence of the larger sex that specifically harms either the smaller sex or the larger sex, an adjustment towards the smaller sex is predicted. In addition to the expectations of Fisher's theory of population-wide equal parental investment in either offspring sex (Fisher 1930), this may lead to even more investment in the production of the smaller sex in the population, and thus a considerable sex ratio bias towards the smaller sex.

Here our aim is to explore whether nestling quality relates sex-specifically to brood sex compo-

sition in the Eurasian Sparrowhawk *Accipiter nisus* (hereafter referred to as Sparrowhawk). The Sparrowhawk is a small raptor that exhibits extreme reversed sexual size dimorphism. Females are heavier than males within a few days after hatching and reach on average a 1.6 times higher asymptotic body mass, resulting in at least a 1.4 times higher energy demand during the nestling stage and a 1.5 times higher peak energy demand (Vedder *et al.* 2005). In the early nestling stage the young are fed individually by the mother, but when they get older they feed independently and progressively start to compete for food delivered by the parents (Tinbergen 1935, Newton 1978). Therefore we expect a sex-difference in vulnerability to brood composition in the late nestling stage. We test for relations between nestling quality and brood size, brood sex ratio and also hatching date, since large seasonal effects on prey availability may confound nestling competition (Geer 1981, Newton & Marquiss 1984). Interactions with nestling sex are incorporated to focus on sex-specific effects. We use nestling body mass as a measure of quality, which is generally known to reflect future survival probability in birds (reviewed by Gebhardt-Henrich & Richner 1998).

METHODS

Study area and nest visits

Nests were located in the period from 1997 through 2003 in the rural area around the town of Emmen, The Netherlands (52°47'N, 6°55'E). In 2003 we also located nests in the area around Groningen and Zuidlaren, as part of a study on sex-specific energy intake (Vedder *et al.* 2005). The majority of nests were visited multiple times but only the last measurements, when all nestlings were at least 10 days old, were used in the present analyses. We measured wing length with a ruler to the nearest mm and weighed nestlings with a 300-g spring balance (Pesola) to the nearest gram. Nestlings were sexed based on body size from 10 days of age onward, when the sexes are unmistakably different (Fig. 1; OV, unpubl. data). We deter-



Figure 1. Typical Eurasian Sparrowhawk nest in the study plot of Emmen, with three male and two female chicks. In front a partially plucked Starling, 23 June 2003 (photo O. Vedder & A.L. Dekker).

mined brood size and sex ratio as the number of nestlings and the proportion of males in the nest present during the last visit. Hatching date is equivalent to the date of hatching of the oldest nestling, as observed directly in 2003 and estimated in all other years by ageing the oldest nestling by wing length according to Vedder & Dekker (2004). The frequent nest visits in 2003 allowed us to fit individual-specific logistic growth curves and thus to estimate asymptotic body mass for each individual in the subset of 2003 (for more details see Vedder *et al.* 2005).

Body mass index and statistics

To adjust for differences in age of nestlings when body mass was measured we calculated a body mass index (BMI) based on the sex-specific relations between wing length and body mass. Because wing length still increases when asymptotic body mass has been approached, this relation is best predicted by a quadratic curve, for males ($F_{2,252} = 141.56$, $P < 0.001$) and females ($F_{2,252} = 381.85$, $P < 0.001$) (Fig. 2). Con-

sequently, BMI is calculated as the relative difference between the measured body mass (m , grams) and the sex-specific predicted body mass (p , grams): $BMI = ((m - p) / p) \times 100\%$.

Structural growth (as wing length) is much less affected by food shortage than growth in body mass (Schew & Ricklefs 1998, van der Ziel & Visser 2001, Moe *et al.* 2004). Therefore BMI will represent a reliable estimate of age-corrected body mass. This is supported by a significant positive correlation between BMI and the estimated individual-specific asymptotic body mass, within the subset of 2003, for males ($r = 0.843$, $n = 50$, $P < 0.001$) and females ($r = 0.918$, $n = 51$, $P < 0.001$).

We tested for the effects of brood size, brood sex ratio, hatching date and their interaction with the sex of the nestling on the variation in BMI with hierarchical linear models in the MLwiN program, version 1.10 (Rasbash *et al.* 2000). These models accommodate unbalanced data and allow analyses of variances and covariances, while simultaneously taking the nested structure of individuals within a nest into account. Hierarchical levels in the models were year, nest and individual, respectively. Significance was tested using the increase in deviance (Δ deviance), when a variable was removed from the model, which follows a χ^2 -distribution (Wald statistic). Non-significant variables ($P > 0.05$) were excluded from the model by stepwise backwards elimination. All other analyses were performed with SPSS, version 11.5. P -values are two-tailed, and means are presented \pm SE.

RESULTS

We sampled 120 broods that were successful until all nestlings were old enough to be sexed. These broods contained 483 nestlings (mean brood size = 4.03 ± 0.13). Of these nestlings 255 (52.8%) were male, which was not significantly different from an even sex ratio (binomial test, $P = 0.237$). At sampling the mean age of these nestlings was 18.2 ± 0.17 days, and all nestlings were included in the subsequent analyses.

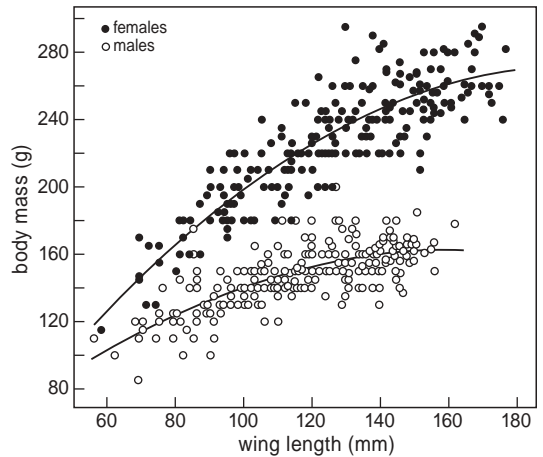


Figure 2. Body mass plotted against wing length for male and female nestling Sparrowhawks. The solid lines represent the sex-specific least squares quadratic regression lines for males ($y = 1.804x - 0.006x^2 + 14.790$) and females ($y = 2.983x - 0.008x^2 - 25.178$).

BMI significantly decreased with the hatching date of the brood (Table 1). The sex ratio of the brood was positively correlated with BMI, i.e., nestlings were in better condition in male dominated broods (Table 1). The interactions of hatching date and sex ratio with nestling sex were rejected from the model (Table 1), suggesting that these effects did not differ between the sexes. In contrast, the significant interaction term between sex and brood size (Table 1) indicates a sex-difference in the effect of brood size on BMI.

To further evaluate this sex-specific effect, we tested the same variables (brood size, sex ratio, hatching date) in one model for each sex separately. In males, all of the tested variables were rejected from the model (Fig. 3C, D). In females, both brood size and sex ratio significantly explained variation in BMI. Female BMI decreased significantly with brood size (Δ dev = 17.21, $P < 0.001$, parameter estimate = -2.52% (± 0.58); Fig. 3A) and increased with brood sex ratio (Δ dev = 10.63, $P = 0.001$, parameter estimate = $+10.07\%$ (± 3.04); Fig. 3B). Hatching date was rejected from the model ($P = 0.096$).

Table 1. Model obtained by backwards elimination in a multilevel regression analysis with nestling body mass index as dependent variable. Values of rejected variables are those before they were (stepwise) removed from the model.

Variable	Δdev	df	P	Estimate (SE)
Sex	13.16	1	< 0.001	-9.13 (2.51)
Brood size	14.88	1	< 0.001	-3.61 (0.93)
Brood sex ratio	7.283	1	0.007	+5.90 (2.17)
Brood hatching date	5.266	1	0.022	-0.19 (0.08)
Sex \times Brood size	10.22	1	0.001	+1.68 (0.53)
Rejected interactions				
Sex \times Brood hatching date	0.166	1	0.684	-0.04 (0.09)
Sex \times Brood sex ratio	2.810	1	0.094	-4.70 (2.82)

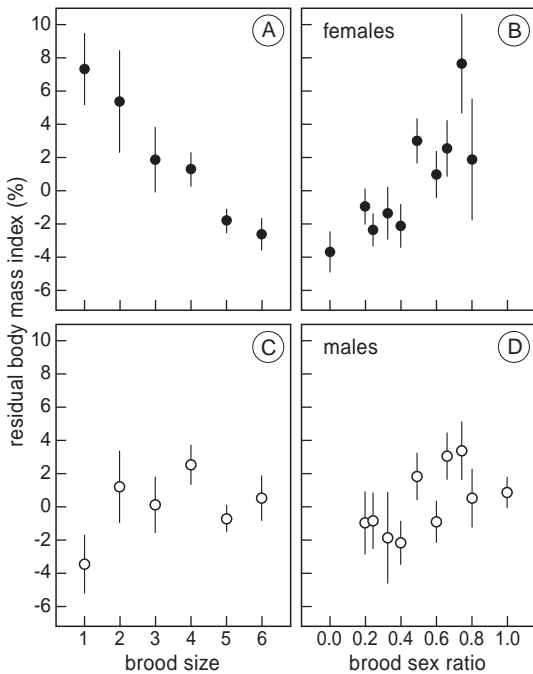


Figure 3. Residual BMI \pm SE plotted against brood size for females and males (A and C), and plotted against brood sex ratio (the proportion of males) for females and males (B and D). BMI plotted against brood size has been corrected for the sex-specific effects of brood sex ratio, and BMI plotted against brood sex ratio has been corrected for the sex-specific effects of brood size.

DISCUSSION

We observed a decrease in body mass of nestling Sparrowhawks with an advancing hatching date of the brood. This is not surprising, considering that food availability for the parents declines later in the season (Newton & Marquiss 1984). Also, inexperienced parents or parents in poor condition may be unable to start early in the season, leading to a seasonal decline in provisioning rates between broods (Geer 1981, Newton *et al.* 1983).

Because Sparrowhawk nestlings differ in food requirement between the sexes (Vedder *et al.* 2005), both the size and the sex ratio of a brood determines the required amount of food provisioned by the parents. In order to observe an effect of brood sex composition on individual nestlings, without experimental manipulations of brood size or sex ratio, Sparrowhawk parents should not adjust their provisioning rate exactly proportionally with brood demand, or vice versa. Hence, a positive effect of the proportion of males in addition to the negative effect of brood size on nestling body mass confirms our expectations and indicates that the requirement to observe these effects is met. This suggests that Sparrowhawk parents do not only face a trade-off between brood size and offspring quality, but also a trade-off between brood sex ratio and offspring quality, as expected from life history theory (Dijkstra *et al.* 1990, Stearns 1992, Dijkstra *et al.* 1998).

The significant interaction effect between sex and brood size on body mass is in accordance with previous findings that in Sparrowhawks female nestlings showed a stronger decline in daily metabolisable energy intake with increasing brood size compared to males (Vedder *et al.* 2005). Such a sex difference may result from two different processes. Firstly, when the food requirement of the brood is high parents might actively economize on females by selectively feeding males. Secondly, males may have a competitive advantage over females in obtaining food, relative to their requirement. Since during the late nestling stage the parents progressively leave the prey on the nest for the nestlings to feed for themselves, instead of

feeding individual nestlings, and young males develop several motorical skills faster than females (Newton 1978), we would argue in favour of the latter process. Regardless of the mechanism, our data provide evidence that parental investment is shifted towards the smaller sex when brood size increases. The result of female body mass being negatively affected by an increasing brood size and a decreasing sex ratio, while male body mass was not, strongly suggests that this shift in investment is caused by a greater total food demand of the brood (i.e., brood size and sex ratio). Therefore, we conclude that in the case of Sparrowhawks individuals of the larger sex (females) are more likely to be affected by the number and sex of their siblings than males.

Although the larger sex is commonly considered to be more sensitive to environmental conditions, as an effect of the greater nutritional requirements (Clutton-Brock *et al.* 1985), a recent review of sex differences in vulnerability in sexually size-dimorphic altricial birds revealed that in species with large broods the smaller sex was more often the most vulnerable (Råberg *et al.* 2005). This is explained with the idea that a large brood reinforces the dominance advantage of the larger sex. Our data suggest the opposite to occur in the Sparrowhawk, since body mass of the larger sex (females) declined with brood size. Instead, the benefits of faster development of motorical skills in males (Newton 1978), may increase with increased nestling competition.

Irrespective of which sex is more vulnerable, a sex differential in response to brood sex ratio would predict an adaptive skew towards producing the less harmful sex (Uller 2003, in press). In sexually size-dimorphic birds this would imply a skew towards the smaller sex, because the presence of the larger sex is more likely to negatively affect its siblings due to its higher requirements (Nager *et al.* 2000, Laaksonen *et al.* 2004, this study). Together with basic predictions of Fisher's equal allocation theory (Fisher 1930) this should lead to even larger skews than when parents already balance higher requirements of the larger sex by producing more of the smaller sex. However, a review

considering sex ratios at fledging in sexually size-dimorphic altricial birds, found that skews towards the smaller sex are generally weaker than predicted on the basis of equal allocation alone (Pen *et al.* 2000), even when taking into account that body mass ratios tend to overestimate ratios of food consumption (Krijgsveld *et al.* 1998). Also among falconiformes, where females are generally larger than males, overall sex ratio biases towards males are not common (Olsen & Cockburn 1991, Krackow 1993). The Sparrowhawk is no exception, since reports of significant population sex ratio biases at fledging are absent, although large sample sizes were investigated (Newton & Marquiss 1979, Newton & Rothery 2000, Risch & Brinkhof 2002, Bijlsma 2005).

Interestingly, in certain years and in small sub-populations in The Netherlands, presumed to be associated with poor food conditions, significant biases towards more male nestlings were found (van den Burg *et al.* 2002). Also, slightly less sexually size-dimorphic *Accipiter* species do show overall biased nestling sex ratios towards males. Northern Goshawks *Accipiter gentilis* produced 52.5% males in Sweden ($n = 2007$ nestlings; Rytman 2001), 53.3% males in Finland ($n = 7831$; Byholm *et al.* 2002) and 55.0% males in The Netherlands ($n = 6862$; Bijlsma 2005) and a population of Cooper's hawks (*Accipiter cooperii*) in Wisconsin (USA) produced 54.2% males ($n = 1337$; Rosenfield *et al.* 1996). However, these results can not be interpreted as evidence for adaptive sex allocation in these species, since they are also expected when increased vulnerability of females leads to higher nestling mortality among females or when female-biased broods are more likely to fail and thus have a lower chance to be detected. Only, for Finnish Goshawks it is reported that partial brood loss did not systematically alter the brood sex ratios (Byholm 2005).

Why then, do Sparrowhawks not adjust offspring sex ratios towards males on a population-wide scale? Two basic, not mutually exclusive, answers can be put forward to this question. Firstly, it has been shown that opposite selection pressures between populations can generate large

differences in sex allocation strategies applied by parents (Badyaev *et al.* 2002). Therefore, it may well be that there are selection pressures towards the production of females in the studied populations that we do not take into account (Olsen & Cockburn 1991). Secondly, potential mechanisms for birds to alter offspring sex ratios could be too costly or impossible for Sparrowhawks. Most studies that reported large sex ratio biases in birds involved species that lay only 1 or 2 eggs per clutch (Ewen *et al.* 2004), suggesting that the control over offspring sex diminishes with a greater clutch size (Pike 2005). When offspring sex ratio is assumed to be fixed, game theory models predict that parents should invest more in the more requiring sex, even when Fisher's equal allocation theory (Fisher 1930) is taken into account (Lessells 1998). Hence, it would not benefit parents to ignore or kill individual nestlings of the larger sex to balance investment between the sexes.

In short, our result of nestlings in female dominated broods acquiring less body mass, predicts an even more male-biased overall sex ratio as expected on the basis of Fisher's equal allocation theory (Fisher 1930) alone. Since there is no evidence that the overall sex ratio in Sparrowhawks deviates from parity, a discrepancy between theoretical predictions and empirical results emerges. Experimental manipulations of brood sex ratio and subsequent monitoring of parents and offspring may provide more insight, but it is questionable whether it can provide a complete solution, as the optimal individual strategy is largely dependent on the operational sex ratio (which is largely determined by the strategy of others and far more difficult to manipulate). Darwin (1874) could be right after all, when, dealing with why sex ratios should be even, he famously wrote: "I now see that the whole problem is so intricate that it is safer to leave its solution for the future".

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SAMENVATTING

Bij vogels wordt algemeen aangenomen dat ouders met extra jongen in het nest niet evenredig meer moeite zouden moeten doen om de jongen van voedsel te voorzien. Hiermee zou hun eigen overleving en dus de totale jongenproductie gedurende hun leven immers negatief worden beïnvloed. Een gevolg hiervan is dat nesten met grote broedsels vaak jongen in relatief slechtere conditie bevatten. In theorie zou hetzelfde principe ook kunnen opgaan wanneer een van de geslachten in het nest meer voedsel nodig heeft. Dat zou dan leiden tot jongen in betere conditie wanneer er minder jongen van het 'dure' geslacht in het nest zitten. Wij hebben dit onderzocht bij de Sperwer *Accipiter nisus*, een soort waarbij vrouwelijke nestjongen, gemiddeld 40% meer energie verbruiken dan mannelijke. Het bleek dat individuele jongen in de late nestfase een lager (seksespecifiek) gewicht hadden wanneer ze in grotere broedsels en in broedsels met een groter aandeel vrouwen zaten. Vrouwen hadden hier meer last van dan mannen. Een groter aandeel vrouwen in het nest lijkt dus vooral de vrouwen zelf negatief te beïnvloeden.

De theorie voorspelt in zo'n geval dat ouders hiervoor zouden moeten compenseren door minder vrouwen te produceren. Naast de voorspelling dat ouders op populatieniveau evenveel zouden moeten investeren in de productie van beide sekses, zou dit moeten leiden tot een aanzienlijk grotere productie van mannen in de populatie. Echter, ondanks grote steekproeven werd nergens een populatie met een significant mannenoverschot onder de nestjongen aangetroffen. Deze ogenschijnlijke tegenstelling tussen theorie en praktijk zou kunnen worden verklaard door hoge ouderlijke kosten verbonden aan het manipuleren van de sekseratio in het nest, of door eventuele selectievoordelen van het produceren van dochters.

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