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Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism

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Adaptive sex-ratio theory predicts that parents should overproduce the more beneficial offspring sex. Based on a recent experimental study of lesser black-backed gulls, we tested this hypothesis with the great skua, *Catharacta skua*, a bird species closely related to gulls but where females are the larger sex. When in poor body condition, the gulls overproduced daughters, the smaller and more viable sex under those circumstances. To discriminate between a mandatory physiological overproduction of female (i.e. non-male) eggs versus the overproduction of the smaller and presumably more viable sex, we conducted an egg-removal experiment with the great skua. Since the males are smaller, larger size and being male are separated. Through egg removal we induced females to increase egg production effort. Eggs were sexed using a DNA-based technique. Manipulated pairs produced a significant male bias at the end of the extended laying sequence, while the sex ratio in the control group did not differ from unity. Our results present an example of facultative sex-ratio manipulation and support the hypothesis that in sexually dimorphic birds parents overproduce the smaller sex under adverse conditions.

Keywords: primary sex ratio; reversed size dimorphism; environmental sensitivity; egg-removal experiment; body condition

1. INTRODUCTION

In recent years, several studies have given strong evidence that birds can adjust the sex ratio of their offspring in relation to environmental conditions (Ellegren *et al.* 1996; Appleby *et al.* 1997; Komdeur *et al.* 1997; Nager *et al.* 1999; Sheldon *et al.* 1999). The theory behind sex-ratio adjustment hinges on the observation that an environmental variable can have different effects on the reproductive value of male and female offspring, and hence the sex-ratio bias is expected to be adaptive (Trivers & Willard 1973; Sheldon *et al.* 1998). Such environmental effects on offspring reproductive value have been observed in a number of species, for example in relation to territory quality (Seychelles warbler, *Acrocephalus sechellensis*; Komdeur *et al.* 1997), paternal attractiveness (collared flycatcher, *Ficedula albicollis*; Ellegren *et al.* 1996), or clan size in mammals (spotted hyena, *Crocuta crocuta*; Holekamp & Smale 1995). A common factor across a wide range of species is differential sensitivity to adverse conditions, which often results in sex-biased mortality (Røskaft & Slagsvold 1985; Clutton-Brock *et al.* 1985; Griffiths 1992). In birds, males generally show higher mortality than females (Howe 1977; Røskaft & Slagsvold 1985; Breitwisch 1989; Griffiths 1992; Nolan *et al.* 1998). Since males are typically larger than females, this has led to the hypothesis that males are more vulnerable to adverse conditions due to their relative size and the size-linked higher energy demand (Clutton-Brock *et al.* 1985). Studies on species where males are not the larger sex support this hypothesis. In an experimental study on a monomorphic species, no sex-linked differences in performance could be detected (Sheldon *et al.* 1998), and observational data on a bird with reversed sexual size dimorphism reported female-biased nestling mortality (Torres & Drummond 1997).

A recent study on lesser black-backed gulls, *Larus fuscus*, a species with male-biased size dimorphism, has given experimental evidence for a link between poor maternal condition, male-biased nestling mortality, and a female-biased primary sex ratio (Nager *et al.* 1999). Mothers in poor body condition overproduced daughters, which had a higher survival probability than sons under those circumstances. Even though this experiment suggests a directional overproduction of daughters due to their smaller size, the possibility of physiological constraints causing a skew towards daughters under food stress cannot be excluded. Conducting an experiment similar to the gulls in a species where females are the larger sex would be a strong exploration of the mechanistic versus the facultative sex-ratio adjustment hypothesis. If mothers in poor condition show a mandatory overproduction of female eggs, then we also expect to find this pattern in a species where the females are larger than males. However, if the gulls produced more daughters because they are the smaller and less vulnerable sex, then we would predict a similar overproduction of the smaller sex, i.e. of males in this case.

In order to distinguish between these hypotheses, we performed an egg-removal experiment with great skuas, *Catharacta skua*. Great skuas are closely related to gulls (Cohen *et al.* 1997). Unlike the gulls, however, they show reversed sexual size dimorphism, with females being on average 10% larger than males (Furness 1987). Through continuous egg removal we induced mothers to lay extended clutches and thus increased the amount of energy invested in egg production. Great skuas normally lay clutches of two eggs (Furness 1987), but produced on

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average three times as many eggs due to our manipulation. This elevated investment negatively affects maternal condition (Monaghan *et al.* 1998; Veasey *et al.* 2001), and female gulls in poorer body condition produced less viable offspring (Nager *et al.* 2000) and showed a lower offspring rearing capacity (Monaghan *et al.* 1998). In order to counteract the effects of egg laying on maternal condition, we supplied a second group of females whose eggs were continuously removed with supplementary food during egg formation.

We investigate the primary sex ratio of eggs laid by females with declining body condition and that produced by the fed group. If birds manipulate offspring sex ratio in relation to the size of their offspring, rather than always favouring daughters under poor conditions, we predict an increase in the proportion of sons as egg production effort increases in the unfed skuas. No sex-ratio bias is expected for the fed birds, since their condition is unlikely to decline by a large degree through the experiment.

2. METHODS

The study was carried out at a large colony of great skuas in Foula, Shetland (60°08′ N, 2°05′ W), during May and June 1999. We used 70 pairs of great skuas for our experiment and carried out daily nest checks prior to and during egg laying. Ninety-two of our study birds were already ringed with unique colour combinations, and the other 48 could mostly be identified through individual plumage markings. From these nests every new egg was removed within 48 h of laying, which induced the birds to lay further eggs. The minimum observed time-span needed by great skuas to produce replacement eggs after natural clutch loss is 10 days (S. Votier and S. Bearhop, personal communication). We therefore report the number of females with or without inter-egg intervals of 10 days or more. Egg removal continued until birds stopped re-laying. Since study pairs remained on their territories for several weeks after the removal of the last egg, we could be sure that they had not changed partner or territory during or directly after the experiment. Thirty-eight randomly assigned study pairs received daily portions of supplementary food from at least 10 days prior to laying of the first egg. We fed them with 400 g of tinned cat food per pair per day, which contained an average of 1100 kJ, equivalent to *ca.* 30% of the daily energy need of one pair (Ratcliffe 1993). Since the males undertake most of the foraging and then provide food for the female (Furness 1987), it did not matter which of the two partners was present at the time of feeding. In order to avoid the theft of food by non-experimental birds, feeding took place in the late evening, a time with generally high territorial attendance. All pairs readily accepted the food and, due to the individual markings, we were sure that only target birds took the food. One of our original pairs in the unfed group abandoned the breeding attempt after the removal of the first egg, but stayed and defended its territory during the remainder of the breeding season. This pair was not included in any of the following analyses.

Egg length and breadth were measured and egg volume index was computed by $(\text{breadth}^2 \times \text{length})/1000$. Removed eggs were artificially incubated for approximately 5 days. The complete natural incubation period is 29 days. On day 5 eggs were opened, the embryos removed, stored in a buffer containing 50 mM EDTA, 50 mM Tris and 2% SDS, and frozen at −20 °C. For sexing we used the method described by Griffiths *et al.* (1998), but used primers PF31 (5′-TGAAG TATCGCCAGTTYCC-3′) and PR32 (5′-CTTCCTCA ATTCCCCTTTDAT-3′) at an annealing temperature of 55 °C. Sexing of eggs that had not developed a visible embryo was inconsistent, and it is not clear whether the results obtained are reliable (for example, because of possible contamination by sperm). Therefore, those eggs were not included in the analysis. Sex ratios are given as the proportion of males.

Except for one pair in the fed group, which only laid two infertile eggs, a final clutch size of three was the minimum produced by all pairs. This gave us a final sample size of 37 fed pairs and 31 unfed pairs for the sex-ratio analysis. To prevent bias towards pairs that had laid a high number of eggs, we included three eggs of all pairs in the analysis: the first, middle and last egg of the laying sequence. Middle eggs in sequences with an even egg number were selected following a table of random numbers. By including eggs of the same relative position within each laying sequence, we aimed to use eggs of a similar biological significance for each female. Any eggs laid between these three positions are referred to as intermediate eggs: 'intermed1', between first and middle; and 'intermed2', between middle and last egg. In some cases, particularly later, eggs were inadvertently left with the parents and were therefore not available for analysis. Whenever the sex of the first or last egg was not known, we used the sex of the egg next to it in the laying sequence, provided it was still laid during the same third of the clutch (see also Nager *et al.* 1999). We had to substitute 2 of 68 first eggs and 10 of 46 last eggs (six unfed and four fed pairs). The percentage of eggs for which the sex could not be determined due to the lack of a visible embryo was not different between the fed and the unfed group (fed, 84.4% sexed, $n = 224$; unfed, 87.2% sexed, $n = 179$; G-test, $G_{\text{adj}} = 0.621$, d.f. = 1, $p = 0.43$). To analyse sex ratios and egg viability between treatment groups we fitted a general linear mixed model (GLMM) with a binomial error structure (Schall 1991; Kruuk *et al.* 1999), using the Genstat 5 package, version 4.1 (Numerical Algorithm Group Ltd, Oxford, UK). As fixed factors we initially included treatment, egg position (first, middle, last) and laying date, plus all the ensuing two-way interactions, but only statistically significant interactions are reported. We incorporated female identity as a random factor, in order to control for individual effects, thereby accounting for the problem of pseudo-replication. It is quite common with empirical data that the residual variation of the fitted logistic regression model deviates from the binomial sampling variation assumed by the model (Williams 1982; Collett 1991). This is what we also observed when analysing the current dataset. Therefore, we included estimation of the dispersion parameter in the GLMM fitting. The significance of the explanatory variables was determined by their Wald statistics (χ^2-distributed). All other statistical analyses were performed using SPSS for Windows, version 9.0 (SPSS Inc., Chicago, USA). To calculate sex ratios of intermediate eggs, females contributed a maximum of one datum point for intermed1 and intermed2, using the combined sex ratio, if several eggs per female fell into the respective category. Data are presented as means ± s.e., with n denoting sample size. All statistical tests are two-tailed and the significance level was set at 5%.

3. RESULTS

Birds in the two experimental groups, i.e. fed and unfed, both laid a mean of around six eggs over the season (fed, 6.6 ± 0.3 eggs, $n = 38$; unfed, 6.0 ± 0.3 eggs, $n = 31$; $t_{67} = 1.4$, $p = 0.17$). For a number of pairs no last egg was available (see § 2), but this does not bias the analysed sample towards larger clutches (number of eggs laid by pairs not included in last egg analysis: unfed, 6.3 ± 0.47, $n = 7$; fed, 6.1 ± 0.44, $n = 15$; number of eggs laid by pairs contributing to analysis, 6.4 ± 0.26, $n = 46$). The minimum number of eggs laid was two, the maximum ten. Inter-egg intervals between consecutive eggs ranged from 2 to 20 days, but were not different between treatment groups (unfed, 5.2 ± 0.42 days, $n = 28$; fed, 5.0 ± 0.17 days, $n = 37$; $t_{63} = 0.72$, $p = 0.47$). Likewise, the occurrence of laying intervals of 10 days or more was equal in the fed and unfed group (0/1/2 10+ intervals: unfed, 13/14/4; fed, 14/18/5; $\chi^2 = 0.12$, d.f. = 2, $p = 0.94$). Timing of laying was also equal for the two groups, the initiation of clutches (median Julian laying date of first egg for fed = 135, $n = 38$; unfed = 134.5, $n = 31$; Mann–Whitney *U*-test, $z = 0.50$, $p = 0.62$), as well as the date when last eggs appeared (median Julian laying date of last egg for fed = 193, $n = 22$; unfed = 191.5, $n = 24$; Mann–Whitney *U*-test, $z = 0.99$, $p = 0.32$). Most experimental birds were not of known age, but they had been observed as breeding birds in previous years. There is no reason to assume an age difference between the two groups. Fed birds did not lay bigger eggs than unfed birds (volume index for first eggs only: fed, 175.5 ± 2.3, $n = 38$; unfed, 172.4 ± 3.2, $n = 31$; $t_{67} = 0.79$, $p = 0.43$) and there was no relation between egg size and embryo sex (GLMM, sex as a function of egg volume, pair identity included as random factor: Wald statistic (χ^2) = 0.5, d.f. = 1, $p = 0.48$, $n = 174$).

The sex ratio of first and middle eggs was not different from unity for either of the two groups (sex ratio of first eggs: fed, 0.54 ± 0.08, $n = 37$, unfed, 0.45 ± 0.09, $n = 31$; middle eggs: fed, 0.52 ± 0.09, $n = 31$; unfed, 0.62 ± 0.09, $n = 29$; figure 1). This was also the case for the last eggs of fed birds (0.45 ± 0.11, $n = 22$; figure 1). However, the unfed birds showed a significant overproduction of males in the last eggs (0.75 ± 0.09, $n = 24$; figure 1). The interaction term of position and feeding treatment in the GLMM is significant (table 1), which means the change in sex ratio from the first to the last egg differs in the two treatment groups. Even though the sex ratio of middle eggs from unfed birds is not different from a 0.5 binomial distribution, the sex ratio over the three egg positions in unfed birds was progressively skewed towards an overproduction of males (GLMM, sex as a function of egg position, unfed pairs only, pair identity included as random factor: Wald statistic (χ^2) = 5.7, d.f. = 1, $p = 0.02$, $n = 85$; effect of position: −0.6747 ± 0.28). By contrast, fed birds produced equal numbers of male and female eggs at the beginning, middle and end of the laying sequence (GLMM, sex as a function of egg position, fed pairs only, pair identity included as random factor: Wald statistic (χ^2) = 0.4, d.f. = 1, $p = 0.53$, $n = 89$). Laying date, as a potential measure of parental quality, did not have a significant impact on the sex ratio produced by either group (table 1). The probability of finding an embryo did not differ between treatments and was unrelated to egg position (GLMM, presence of embryo as a function of egg position ($\chi^2 = 2.2$, d.f. = 1, $p = 0.14$); treatment ($\chi^2 = 0.1$, d.f. = 1, $p = 0.75$); position × treatment ($\chi^2 = 1.9$, d.f. = 1, $p = 0.17$); pair identity was included as a random factor).

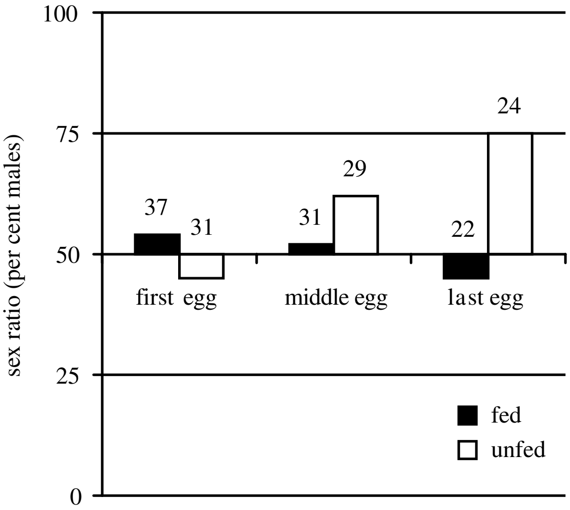

Figure 1. Mean sex ratio of first, middle and last eggs of fed and unfed birds. Sex ratios for fed pairs in all three positions are not different from a 0.5 binomial distribution (binomial test, exact values; $p > 0.7$ for all three). Sex ratio of last ($p = 0.023$), but not of middle or first eggs ($p > 0.2$ for both) of unfed pairs is significantly different from a 0.5 binomial distribution, and also from the sex ratio of the fed pairs' last eggs ($\chi^2 = 4.2$, d.f. = 1, $p = 0.04$). The interaction of feeding treatment and position is significant (see table 1). Sex ratios of intermediate eggs are: unfed intermed1, 0.42 ± 0.08, $n = 26$ females, 43 eggs; intermed2, 0.51 ± 0.11, $n = 18$ females, 28 eggs; fed intermed1, 0.44 ± 0.07, $n = 34$ females 59 eggs; intermed2, 0.44 ± 0.09, $n = 25$ females, 38 eggs.

4. DISCUSSION

Female great skuas produced an offspring sex ratio in favour of sons, the smaller sex, when they were induced to increase egg production effort. Birds that were subjected to the same experimental manipulations but received supplementary food did not produce a skewed sex ratio. These results are strong evidence for facultative sex-ratio adjustment in relation to maternal body condition. The fact that mothers who received supplementary food did not produce a sex ratio different from unity demonstrates that the result in the unfed group was neither a seasonal nor a sequence effect. Since our two experimental groups did not differ in any aspect other than the receipt of supplementary food, it is clear that the overproduction of male eggs by the unfed birds was induced by the effects of continuous laying under natural feeding conditions. Our results show that the change in offspring sex ratio is not simply produced by a physiological process which favours female eggs when mothers are in poor body condition. The skew we observed is opposite to the one produced by lesser black-backed gulls with regard to offspring sex, but in the same direction with regard to size dimorphism (Nager *et al.* 1999). The gulls were subjected to a similar treatment, but overproduced daughters (the smaller sex) at the end of the extended laying sequence when not supplementarily fed. Our results therefore clearly show a sex-independent overproduction of the smaller offspring sex by mothers in poor body condition, and are consistent with the predictions of the facultative sex-ratio adjustment hypothesis. An

Table 1. Results of a GLMM with a binomial error structure.

(Sex was examined as a function of egg position (first, middle or last egg of extended clutch) and parental feeding treatment (fed or unfed, $n = 174$ eggs). The initially included explanatory variable 'laying date' did not contribute significantly to the model (Wald statistic (χ^2) = 0.1, d.f. = 1, $p = 0.75$). Breeding pair identity was included as a random factor (average effect 0.7149 ± 0.44) and the data were scaled according to a dispersion parameter of 0.8795 ± 0.12.)

	average effect	s.e.	Wald statistic (χ^2)	d.f.	p
position	−0.2186	0.1926	1.3	1	0.25
feeding treatment	0.3245	0.3667	0.7	1	0.40
position × feeding treatment	0.8510	0.3864	4.8	1	0.03

alternative explanation for the skewed sex ratio in 5-day-old eggs might be differential early embryo mortality. This possibility cannot be excluded, but is unlikely. The probability of finding an embryo was the same in both groups, and we therefore have no reason to assume that differential mortality would have operated only in one of the groups. Furthermore, no differences in embryo mortality between sexes have been reported for birds so far, even in species that show differential nestling mortality (e.g. Nager *et al.* 1999). We therefore suggest that differential production is the more likely explanation for the observed sex-ratio bias.

In both Nager *et al.*'s (1999) and our own study, poor conditions were created by inducing females to produce extra eggs. It has been shown that egg production is costly for female birds (Houston *et al.* 1983; Monaghan & Nager 1997; Veasey *et al.* 2001). Even the production of one or a few additional eggs significantly reduced protein condition of laying females (Monaghan *et al.* 1998; Veasey *et al.* 2000). Our experimental females produced on average three times more eggs than the normal clutch of two. Extended egg production had a negative effect on skua body condition (E. Kalmbach, unpublished data). Even though we cannot quantify the extent to which the supplementary food counteracted these negative effects, other studies have shown that supplementarily fed birds laid larger and more eggs (Bolton *et al.* 1993; Nager *et al.* 1999), both usually correlated with body condition (e.g. Martin 1987). A trend in the same direction, with more eggs laid by supplemented skuas, was observed in this study. Therefore, it is likely that at the end of laying, maternal body condition was poorer in the unfed group and was the proximate cause for the change in offspring sex ratio.

Individual quality of females is likely to have varied within each treatment group. High-quality birds were probably less affected by our treatment than lower-quality individuals in the same group. We tried to control for this variation by including laying date in our model, which in this species has been shown to correlate with several reproductive traits (Catry *et al.* 1998). We could not find a significant effect of laying date on sex ratio, but it is likely that intra-group differences in individual female quality are contributing to the extra binomial variance we found in our data. Since harsh circumstances highlight such differences in quality, performance in the stressed, i.e. unfed group, is likely to have varied to a higher degree than within the fed group.

The fact that both gulls and skuas overproduced the smaller offspring, irrespective of sex, strongly indicates that larger size *per se* affects offspring value under poor conditions. This is particularly interesting since other mechanisms have been suggested for sex-specific offspring performance. For instance, Folstad & Karter (1992) formulated the immunocompetence handicap hypothesis (ICHH), which states that males are more sensitive to adverse conditions due to elevated levels of androgens. Even though usually argued to relate to testosterone, the above argument would apply equally to any biologically active substances that are linked to the male phenotype and have negative effects on physiological functions (Grossman 1985; Folstad & Karter 1992). However, since males are often the larger sex in birds and mammals, it is difficult to separate size from other aspects of the male phenotype, in order to test the ICHH. The indications of our study are that hormonal effects of male phenotype on vulnerability may be small in comparison with the effects of size.

What benefits could the parents expect from producing predominantly the smaller sex during adverse conditions? Generally, it is thought that the smaller sex needs less energy in order to achieve normal growth (Lindén 1981; Slagsvold *et al.* 1986; Krijgsveld *et al.* 1998). This would mean that by producing a cheaper chick, parents could allocate more energy to body reserves. Likewise, with the same amount of energy they could produce a higher-quality fledgling, or, alternatively, may only be able to successfully raise chicks of the cheaper sex due to limited resources (Nager *et al.* 2000). However, Torres & Drummond (1999) concluded from their study on blue-footed boobies, *Sula nebouxii*, that despite their larger size, daughters did not need more energy to achieve normal growth. This suggests that there might be factors involved other than energy demand during the nestling phase. An important aspect for sex-specific viability may lie within the eggs themselves. In the lesser black-backed gull, the survival probability of sons (the larger sex) hatching from late eggs of an extended laying sequence was significantly decreased compared with that of their sisters, after controlling for parental condition (Nager *et al.* 1999). In natural conditions both parental condition and egg quality would operate at the same time.

Species with reversed sexual size dimorphism offer an important opportunity for investigating the role of size and other aspects of phenotype on offspring vulnerability. Our results on the great skua suggest that birds might be able to adjust the primary sex ratio accordingly. They also indicate that size plays possibly the most important role for differential performance of offspring. If female mortality in our study species is shown to be higher than male mortality under poor conditions, this could explain the pattern of offspring sex ratio observed in this study.

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REFERENCES

Appleby, B. M., Petty, S. J., Blake, J. K., Rainly, P. & MacDonald, D. W. 1997 Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? *Proc. R. Soc. Lond.* B **264**, 1111–1116.

Bolton, M., Monaghan, P. & Houston, D. C. 1993 Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. *Can. J. Zool.* **71**, 273–279.

Breitwisch, R. 1989 Mortality patterns, sex ratios and parental investment in monogamous birds. *Curr. Ornithol.* **6**, 1–50.

Catry, P., Ratcliffe, N. & Furness, R. W. 1998 The influence of hatching date on different life-history stages of Great Skuas *Catharacta skua*. *J. Avian Biol.* **29**, 299–304.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1985 Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**, 131–133.

Cohen, B. L. (and 15 others) 1997 Enigmatic phylogeny of skuas (Aves: Stercorariidae). *Proc. R. Soc. Lond.* B **264**, 181–190.

Collett, D. 1991 *Modelling binary data*. London: Chapman & Hall.

Ellegren, H., Gustafsson, L. & Sheldon, B. C. 1996 Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proc. Natl Acad. Sci. USA* **93**, 11 723–11 728.

Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.

Furness, R. W. 1987 *The Skuas*. Calton, Staffs., UK: T&AD Poyser.

Griffiths, R. 1992 Sex-biased mortality in the Lesser Black-backed Gull *Larus fuscus* during the nestling stage. *Ibis* **134**, 237–244.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998 A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075.

Grossman, C. J. 1985 Interactions between the gonadal steroids and the immune system. *Science* **227**, 257–261.

Holekamp, K. E. & Smale, L. 1995 Rapid change in offspring sex-ratios after clan fission in the spotted hyena. *Am. Nat.* **145**, 261–278.

Houston, D. C., Jones, P. J. & Sibly, R. M. 1983 The effect of body condition on egg laying in female Lesser black-backed gulls *Larus fuscus*. *J. Zool., Lond.* **200**, 509–520.

Howe, H. F. 1977 Sex-ratio adjustment in the common grackle. *Science* **198**, 744–746.

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.

Krijgsveld, K., Dijkstra, C., Visser, H. G. & Daan, S. 1998 Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Circus aeruginosus* nestlings. *Phys. Zool.* **71**, 693–702.

Kruuk, L. E. B., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M. & Guinness, F. E. 1999 Population density affects sex ratio variation in red deer. *Nature* **399**, 459–461.

Lindén, H. 1981 Growth rates and early energy requirements of captive juvenile capercaillie, *Tetrao urogallus*. *Finnish Game Res.* **39**, 53–67.

Martin, T. E. 1987 Food as a limit on breeding birds—a life history perspective. *A. Rev. Ecol. Syst.* **18**, 453–487.

Monaghan, P. & Nager, R. G. 1997 Why don't birds lay more eggs? *Trends Ecol. Evol.* **12**, 270–274.

Monaghan, P., Nager, R. G. & Houston, D. C. 1998 The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proc. R. Soc. Lond.* B **265**, 1731–1735.

Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. 1999 Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl Acad. Sci. USA* **96**, 570–573.

Nager, R. G., Monaghan, P., Houston, D. C. & Genovart, M. 2000 Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). *Behav. Ecol. Sociobiol.* **48**, 452–457.

Nolan, P. M., Hill, G. E. & Stoehr, A. M. 1998 Sex, size, and plumage redness predict house finch survival in an epidemic. *Proc. R. Soc. Lond.* B **265**, 961–965.

Ratcliffe, N. 1993 The age specific performance of great skuas on Shetland. PhD thesis, University of Glasgow, UK.

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.

Schall, R. 1991 Estimation in generalized linear models with random effects. *Biometrika* **78**, 719–727.

Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J. & Sendecka, J. 1999 Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**, 874–877.

Sheldon, B. C., Merilä, J., Lindgren, G. & Ellergren, H. 1998 Gender and environmental sensitivity in nestling Collared Flycatchers. *Ecology* **79**, 1939–1948.

Slagsvold, T., Røskaft, E. & Engen, S. 1986 Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scand.* **17**, 117–125.

Torres, R. & Drummond, H. 1997 Female-biased mortality in nestlings of a bird with size dimorphism. *J. Anim. Ecol.* **66**, 859–865.

Torres, R. & Drummond, H. 1999 Does large size make daughters of the blue-footed booby more expensive than sons? *J. Anim. Ecol.* **68**, 1133–1141.

Trivers, R. L. & Willard, D. E. 1973 Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–91.

Veasey, J. S., Houston, D. C. & Metcalfe, N. B. 2000 Flight muscle atrophy and predation risk in breeding birds. *Funct. Ecol.* **14**, 115–121.

Veasey, J. S., Houston, D. C. & Metcalfe, N. B. 2001 A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *J. Anim. Ecol.* **70**, 20–24.

Williams, D. 1982 Extra-binomial variation in logistic linear models. *Appl. Statist.* **31**, 144–148.