

ORIGINAL ARTICLE

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Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*)

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Abstract Empirical evidence is growing that the offspring sex ratio in birds can be biased in relation to the body condition of parents during breeding. The sex ratio bias may come about because (1) the actual production of the two sexes may be skewed and/or (2) there may be a sex bias in early nestling mortality contingent on parental condition. By manipulating parental condition and giving them a control brood to rear, thereby eliminating effects operating via the eggs, we examined the extent to which parental condition influences the post-hatching survival of male and female lesser black-backed gulls, *Larus fuscus*. We found that the pre-fledging survival of male chicks was strongly reduced in all-male broods reared by parents in poor condition. Pre-fledging survival of female chicks was, however, unaffected by parental condition or brood sex composition. Thus, independently of any production biases, sex differences in nestling mortality alone can bias the offspring sex ratio at fledging in relation to the prevailing rearing conditions. In other studies on gulls we have, however, also shown that females in poor condition at laying preferentially produce female eggs. Clearly a bias in fledging sex ratio can occur within the same species due to a combination of differential production and differential post-laying mortality; the latter can involve a differential effect of poor egg quality on male and female offspring, differential effects of brood sex composition on their survival and a difference in the capacity of parents to rear males and females. All of these processes need to be taken into account in attempting to understand offspring sex ratios.

Keywords Sex allocation · Differential mortality · Rearing conditions · Brood sex composition · Lesser black-backed gull · *Larus fuscus*

Introduction

At first sight, the chromosomal sex determination mechanism of birds and mammals would appear to limit the ability of parents to modify the sex ratio of their offspring (Williams 1979; Charnov 1982; Bull 1983). However, an increasing amount of empirical evidence from both birds and mammals is demonstrating this is not the case (Clutton-Brock and Iason 1986; Emlen 1997; Sheldon 1998). Recent studies have provided evidence for significant biases in offspring sex ratio in relation to the environmental and social circumstances experienced by parents during breeding (e.g. Appleby et al. 1997; Komdeur et al. 1997; Kruuk et al. 1999; Nager et al. 1999; Post et al. 1999; Torres and Drummond 1999). However, the mechanisms underlying such offspring sex ratio biases are poorly understood (Krackow 1995).

There are two routes by which the offspring sex ratio could depart from the 50:50 ratio expected under random segregation of chromosomes. The actual production of the two sexes may be skewed through female-controlled chromosomal segregation, or there may be a sex bias in early mortality (Godfray and Harvey 1986; Krackow 1995). The latter could occur due to selective provisioning of offspring of one sex by the parents, or to differential vulnerability of one sex to poor parental investment or unfavourable rearing conditions (Clutton-Brock 1991). Male and female offspring differ morphologically, physiologically, behaviourally and genetically. They usually differ in their costs to the parents in terms of food demand and their subsequent survival and breeding success (Teather and Weatherhead 1988; Gomendio et al. 1990; Anderson et al. 1993). We may therefore expect mortality schedules between the sexes to differ (Clutton-Brock et al. 1985; Breitwisch 1989). The condition of the parent is likely to be a key factor influencing the dif-

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ferential mortality of male and female offspring through their capacity and/or willingness to provision and rear the more expensive sex. Furthermore, where more than one offspring is present, the sex composition of the sibship may also affect male and female offspring differentially (Edwards and Collopy 1983; Røskaft and Slagsvold 1985; Bortolotti 1986; Ims 1987; Drummond et al. 1991; Golla et al. 1998).

However, the two possible causes of observed sex ratio biases, biased production and differential mortality of the two sexes, are generally difficult to separate (e.g. Post et al. 1999). In particular, there is little experimental evidence that the mortality of male and female offspring is differentially affected by rearing circumstances, an important assumption of the 'differential mortality hypothesis'. To test this, parental condition needs to be experimentally manipulated and the effect of this on the survival of male and female offspring examined.

We have previously shown experimentally in lesser black-backed gulls (*Larus fuscus*), a sexually dimorphic species in which males are 12–17% heavier than females (Cramp 1983), that parents in poor condition produce fewer male offspring (Nager et al. 1999). By cross-fostering of eggs, we have also shown that those male offspring that are produced have poor survival prospects even when raised by parents in good condition, and that a difference in the susceptibility of male and female chicks to poor egg quality is involved (Nager et al. 1999). Here we examine whether the survival of sons and daughters is also influenced by *parental state*, independent of the egg effects already demonstrated. Increasing egg production effort by only one egg reduces female body weight by 5.4% and protein reserves by 5.3% at the end of laying compared to equivalent-sized control females (Monaghan et al. 1998). Thus, increasing egg production effort can be used to manipulate female body condition at the end of laying. We have found that reducing female condition in this way gives rise to a reduction in breeding success (Monaghan et al. 1998). Male lesser black-backed gull chicks are already larger than female chicks at hatching and also grow faster (Griffiths 1992). This suggests that males are the more expensive sex to rear and indeed they have been observed to have a higher post-hatching mortality in some years (Griffiths 1992). We therefore predicted that male offspring raised by parents in poor condition would be less likely to fledge successfully and/or would fledge in poorer condition. Since the survival of chicks may also be influenced by other chicks in the brood, we also examined the extent to which differences in brood sex composition affected the survival of male and female offspring.

Methods

The experiment was carried out at a large colony of about 24,000 pairs of lesser black-backed gulls on Walney Island, Cumbria, UK, in 1997. Study nests were located in the centre of the colony and laying occurred during the early part of the breeding season (26 April to 18 May; laying continued in the colony until June).

Gulls usually lay a clutch of three eggs (Cramp 1983). We increased their egg production effort by removal (under licence from English Nature) of the first-laid egg within 12 h of laying, so that four rather than three eggs were laid. Full details are given in Monaghan et al. (1998). In brief, our experimental group comprised 20 pairs that laid four rather than three eggs and this was compared to a control group of 32 pairs that laid a normal clutch of three eggs and was subjected to the same level of disturbance. The two groups did not differ in their timing of laying or in the size of their first egg. On the day experimental pairs completed laying, their own clutches were replaced with a randomly chosen clutch taken from non-manipulated birds that had completed a clutch of three eggs on that day. Clutches of the control pairs were exchanged in the same way. The size of the eggs reared by control and experimental birds did not differ.

All nests were subjected to the same level of disturbance throughout and followed through incubation and chick rearing until the chicks were 5 weeks old and about to fledge. During hatching, a process that lasts about 1 day, nests were checked daily and individual chicks were marked on the bill with non-toxic paint while still in their egg. We knew therefore the order in which they hatched and from which egg they hatched. We measured body weight and tarsus length of all hatchlings within 24 h of hatching and calculated a body condition index as the residuals of the regression of hatchling weight on tarsus length. The number of chicks per nest was recorded and all chicks measured (body weight and tarsus length) every 4 days until the chicks were 5 weeks old and close to fledging (Bolton 1991). For chicks found dead, the age of death was taken as the age when last seen alive. We calculated the slope of the regression of $\log_{10}(\text{body weight})$ on age during the first 2 weeks (when most growth takes place; Bolton 1991) as a measure of growth rate. Growth rates were calculated for successful and unsuccessful chicks with sufficient numbers of body weight records (at least three).

To identify the sex of the chicks, we collected a droplet of blood (under Home Office licence) from the leg of each bird, using a sterile needle. Blood samples were taken within 24 h after hatching with no ill effects on the chicks. Bird sex was identified from blood cell DNA, using two *CHD* genes (Griffiths et al. 1996). Of the 134 hatchlings, 131 (97.8%) were successfully sexed. We distinguished among three types of broods in our analyses: broods that consisted at hatching only of males, only of females (single-sex broods) and broods with males and females (mixed-sex broods). Because at the time of cross-fostering of entire clutches (those taken from unmanipulated pairs and given either to the control or the experimental pairs) we could not know the sex of the embryos within the transferred eggs, sample sizes for the different brood sex composition types differ between treatment groups.

To analyse variation in sex ratio and chick mortality between the two treatment groups we used generalised linear models with binomial error distributions in GLIM (NAG 1986). We used the number of chicks fledged per brood as the response variable, with the number of hatched chicks per brood as the binomial denominator. Thus broods rather than individual chicks are the units in the analysis. We then carried out analyses of variance with treatment (control and reduced parental condition), brood sex composition (all males, all females and mixed sex) and laying date as factors and used the logit link function to ensure linearity. The statistical significance of explanatory variables was assessed by the change in deviance when that variable was included last in the model. The deviance is distributed asymptotically as χ^2 when the ratio deviance/*df*=1. Since in most of our cases, the ratio deviance/*df* was considerably larger than 1, we tested the significance of response variables by the *F*-ratio between the mean deviance (deviance/*df*) due to the extra parameter and the mean deviance due to the error of the final model including the extra parameter (Crawley 1992). All possible interactions were tested, but we only report significant ($P < 0.05$) interaction terms.

Table 1 Relationship between survival rate of offspring in relation to parental condition (control and experimentally enlarged egg production effort) and brood sex composition (mixed-sex, all-male and all-female broods). Experimental nests raised a foster clutch of three after having laid an experimental clutch of four eggs ($n=20$) whereas controls raised a foster clutch of three after having laid a normal clutch of three eggs ($n=32$). Results are from regression analysis using GLIM with binomial errors and a logit link function (see Methods for details). Only significant interactions are shown

	Deviance	df	F-ratio	P
Null model	106.49	51		
Final model	72.90	46		
Parental condition (PC)		1	0.09	>0.25
Brood sex composition (BSC)		2	0.88	>0.25
PC×BSC		2	3.24	0.049

Results

Overall, $50.6 \pm 4.76\%$ (mean \pm SE) of the hatched chicks were male ($n=52$ nests) and the proportion of all-male, all-female and mixed-sex broods did not differ between the experimental and control group ($G=3.79$, $df=2$, $P=0.15$). Hatching success and body condition of hatchlings did not differ between the two groups, as would be expected given the random allocation of the standard clutches between the treatment groups (see Monaghan et al. 1998 for details). The sex ratio of a brood (% males) at hatching was not related to the number of chicks at hatching (logistic regression with binomial error distribution: $F_{1,50}=2.02$, $P=0.18$). The hatching order of male offspring did not differ between the two groups (Mann-Whitney test, $n=24$ control and 17 experimental broods, $Z=0.17$, $P=0.87$; the remaining 11 broods contained only female offspring).

Laying date did not influence the survival rate of either male or female chicks (male chicks: $F_{1,39}=0.54$, $P>0.25$; female chicks: $F_{1,39}=0.03$, $P>0.25$). Table 1 gives the analysis of the average chick survival rate per brood in relation to the manipulation of parental condition (control and reduced condition) and the brood sex composition (all-male, all-female or mixed-sex broods). The relationship between chick survival and parental condition differed with brood sex composition (Table 1, interaction between brood sex composition and parental condition: $P=0.049$). The significant interaction resulted from a very low survival of chicks in all-male broods raised by parents in reduced condition (11.1%; 95% confidence intervals=2.0–43.8%, $n=7$; Fig. 1) compared to all other brood types. The average survival of males from control broods was 69.4% (95% confidence intervals=51.8–82.8%, $n=24$), and was not influenced by brood sex composition (Fig. 1). In contrast, female chick survival was not influenced by parental condition or brood sex composition ($F_{1,40}=4.05$ and 3.06, respectively, $P>0.05$; overall survival=77.4%, 95% confidence intervals=65.0–86.4%, $n=41$). These data indicate that male chicks in male-biased broods are most vulnerable to poor rearing conditions.

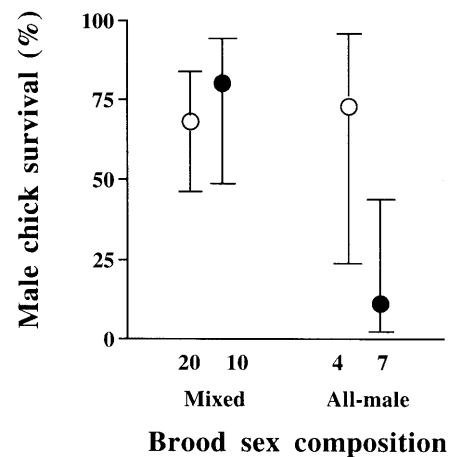


Fig. 1 Average survival rate of male chicks of lesser black-backed gulls in relation to brood sex composition (all-male or mixed-sex brood at hatching) and treatment (*open symbols* control nest, *closed symbols* experimental nests where the female laid one additional egg; *vertical bars* represent the 95% confidence interval). The effect of brood sex composition differed significantly between control and experimental nests (logistic regression model with binomial error and logit link function, interaction between parental condition and brood sex composition: $F_{1,37}=7.68$, $P=0.009$). For experimental nests, the average male survival rate per brood was lower in all-male broods than in mixed-sex broods ($F_{1,15}=13.57$, $P=0.002$). Values along the horizontal axis indicate sample sizes in each group

To examine male and female survival directly, independent of brood sex composition, we compared chick survival in single-sex broods ($n=22$) in relation to parental condition. Again, there was a significant interaction between sex of offspring and parental condition (parental condition: $F_{1,18}=1.55$, $P>0.25$; offspring sex: $F_{1,18}=1.42$, $P>0.25$; interaction: $F_{1,18}=4.76$, $P=0.044$). This was due to significantly fewer male offspring surviving in broods of experimental parents than in broods of control parents ($F_{1,9}=8.74$, $P=0.018$). Parental condition, however, had no significant effect on survival of female offspring ($F_{1,9}=0.41$, $P>0.25$).

All dead chicks from the same brood died at a similar age and thus the ages when chicks were lost were highly repeatable within broods ($r=0.869 \pm 0.011$, $P<0.001$ for 12 nests where two or more chicks died). The timing of mortality of male offspring varied with parental condition (Fig. 2). A similar proportion of males died over the first 15 days in control (26%) and experimental nests (30%). In the last 3 weeks of the nestling period, however, further mortality occurred in experimental nests (39.3% mortality) whereas nearly all males survived in control nests (3.8% mortality). In most cases of chick mortality, the dead chicks were found on their home territory (39 of 44 lost chicks, 88.9%). The proportion of chicks disappearing from the territory were the same for control and experimental nests (Fisher's exact test, one-tailed $P=0.235$). Broods where chicks died had on average lower growth rates than broods where all hatchlings survived (average chick growth rate from $\log_{10}(\text{weight})$ on age in broods with chick mortality= $52.6 \times 10^{-3} \pm$

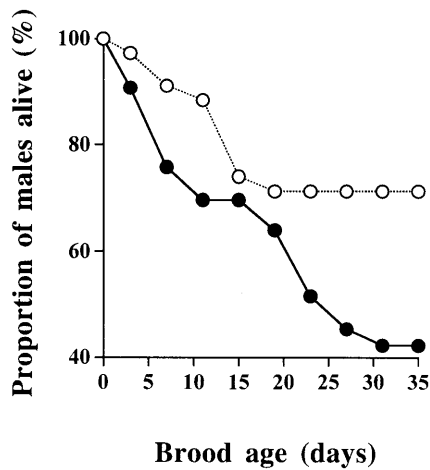


Fig. 2 Average proportion of males per brood still alive in relation to brood age for control nests (open symbols, $n=24$) and experimental nests (closed symbols, $n=17$). Timing of mortality differed significantly between treatments (repeated-measures ANOVA, effect of the interaction treatment by age on absolute number of males alive per nest: $F_{9,31}=2.45$, $P=0.033$)

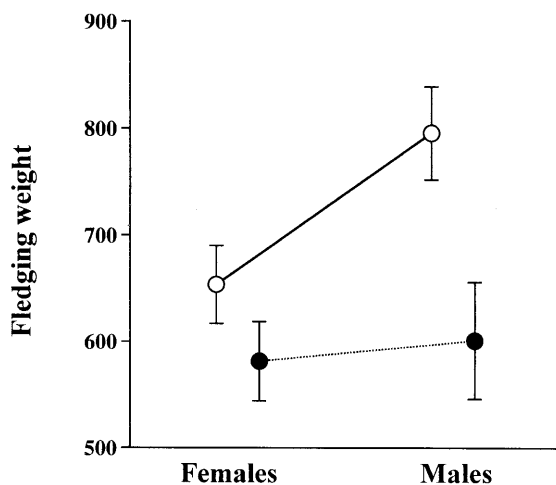


Fig. 3 Average fledging weight of male and female chicks from 23 nests (14 control and 9 experimental nests) that fledged at least one male and one female offspring. The difference in weight between brothers and sisters of the same nest differed between the parental-condition treatment groups (repeated-measures ANOVA, parental condition $F_{1,21}=6.18$, $P=0.021$; sex: $F_{1,21}=11.37$, $P=0.003$; interaction: $F_{1,21}=5.04$, $P=0.036$). Males from control nests were significantly heavier than males from experimental nests (t -test: $t_{21}=3.27$, $P=0.004$), but the weight of females from control and experimental nests did not differ (t -test: $t_{21}=1.15$, $P=0.263$)

2.72×10^{-3} g day $^{-1}$, $n=19$ broods; broods without chick mortality = $57.8 \times 10^{-3} \pm 0.91 \times 10^{-3}$ g day $^{-1}$, $n=32$ broods; t -test, $t_{49}=2.15$, $P=0.037$).

Fledging weight and tarsus length of male and female offspring was compared within broods in order to control for between-family differences in growth. We therefore analysed fledging weight and tarsus length from 14 control and 9 experimental nests that fledged both male and

female offspring. Fledging weights of male, but not female, offspring differed between parental-condition treatments. Relative to their female nestmates, males from experimental nests were significantly lighter than males from control nests (Fig. 3). Tarsus lengths at fledging were similar in control and experimental birds (repeated-measures ANOVA, parental condition: $F_{1,21}=2.56$, $P=0.12$; sex: $F_{1,21}=25.18$, $P<0.001$; interaction: $F_{1,21}=2.20$, $P=0.15$). Thus control males were heavier, but not skeletally larger, at fledging than experimental males, whereas female fledging weight and size were unaffected by the manipulation of parental condition.

Discussion

In lesser black-backed gulls, male chicks are larger than females and survive less well during the nestling stage compared to female chicks (25.8% and 36.5%, respectively; Griffiths 1992). When the condition of the female parent is depressed experimentally, the capacity of the breeding pair to rear chicks is impaired (Monaghan et al. 1998). We demonstrate here that this reduced rearing capacity affects only male offspring, independent of any effects of egg quality. In our control nests, female (77.4%) and male (69.4%) chick survival was similar. Both these survival rates are higher than those found by Griffiths (1992), suggesting that environmental conditions were better in our study colony. This further supports the idea that male chicks are at a survival disadvantage particularly under poor conditions. Furthermore, the male offspring of our experimental pairs that did survive were comparatively lighter, but of similar body size to control chicks. Thus, our male experimental chicks fledged in poorer body condition, which is an important predictor of post-fledging survival (Hochachka and Smith 1991; Magrath 1991).

Male survival during the nestling period was also found to be affected by the sex of their siblings in the experimental but not in the control nests. Thus, a combination of poor parental condition and a male-biased brood sex ratio had a strong effect on the survival of male chicks; males from experimental all-male broods were six times less likely to survive than males from all-male control nests. In contrast, the survival of female chicks was not affected by parental condition or the brood sex composition. Parental condition and the sex ratio in the brood produced clearly have an important impact on offspring sex ratio at fledging through differential mortality in the nest.

Two studies on siblicidal raptors have suggested that sibling sex could affect the survival rate and growth of male and female chicks (Edwards and Collopy 1983; Bortolotti 1986). Neither study, however, could provide direct evidence in support of this suggestion (see Drummond et al. 1991). In contrast, in their very detailed correlative study of blue-footed boobies (*Sula nebouxi*), Drummond et al. (1991) could find no effects of

brood sex composition on growth rate or survival of offspring, thereby supporting the widespread assumption that chick mortality rate is independent of the brood sex ratio (Fiala 1980). Only if the survival of male and female offspring is assumed to be the same under all situations can the sex ratio at hatching be inferred from the sex ratio measured at a later stage. However, in our study this assumption was clearly not met when parental condition was reduced: male mortality was significantly higher in all-male compared to mixed-sex broods. Therefore, in the lesser black-backed gull, comparisons of male and female offspring survival from data combining nests with and without previous nestling mortality have to be interpreted very carefully when only the sex ratio at fledging is known. The assumption is, in fact, untested for most species (Lessells et al. 1996) and inference of the hatching sex ratio from the fledging sex ratio therefore remains problematic in those species.

Biases in offspring sex ratio could be due to two different processes. Parents may adaptively adjust the offspring sex ratio in favour of the sex with the higher fitness return (Trivers and Willard 1973). Alternatively, the sex ratio bias may be a consequence of parental condition or extrinsic factors that affect the survival of the larger, more expensive sex more strongly than the other sex (Clutton-Brock et al. 1985; Weatherhead and Teather 1991; Post et al. 1999; this study). The larger, more expensive sex may be more vulnerable to a food shortage when the parents are unable to provide their brood with sufficient food, or parents of poor condition choose to preferentially feed one sex more than the other (Howe 1977, 1979; Burley 1986; Stamps et al. 1987). If the benefits of faster growth during the nestling period differ between male and female offspring it would be advantageous to the parents to allocate more parental care to the more productive sex. Our experiment does not distinguish between increased vulnerability of males to poor conditions and selective provisioning of female chicks by parents in poor condition, a separation which is very difficult to achieve experimentally (Clutton-Brock 1991). Both effects may occur. Furthermore, parents may also attempt to produce the brood sex composition that favours survival of the largest number of offspring under the prevailing circumstances. Our experiment presented here clearly shows that increased mortality of the larger sex under poorer rearing conditions can skew the fledging sex ratio in the same direction as predicted by the Trivers-Willard hypothesis, without involving a production bias. A significant correlation between offspring sex ratio at fledging and parental or environmental conditions can therefore not distinguish between the two alternative explanations (Post et al. 1999).

In this study, differences between the sexes in the demand for parental resources is most likely to explain the higher mortality of male gull chicks under poor rearing conditions. When one sex has a higher food requirement, poorer rearing conditions have a greater effect on the survival of that sex where either males or females are larger (Howe 1977; Clutton-Brock et al. 1984; Røskoft

and Slagsvold 1985; Slagsvold et al. 1986; Weatherhead and Teather 1991; Torres and Drummond 1997), but not when sexes do not differ in size (Sheldon et al. 1998). The larger sex usually has a higher resource demand during development (Anderson et al. 1993) and older offspring have a higher food demand than younger ones (Clutton-Brock 1991). Therefore, in gulls, older broods and male-biased broods are expected to be more demanding to rear and it is during the period of peak food demand of their brood that poor parental provisioning is most likely to lead to a shortage of food. In this study, average chick growth rates in unsuccessful nests were lower than in nests that fledged at least one young, which suggests that insufficient chick provisioning is the most likely cause of mortality in males from experimental broods. Furthermore, nestling mortality during the period of maximal resource demand (3rd and 4th week of nestling development; Drent et al. 1992; Gabrielsen et al. 1992) was higher in experimental than in control nests, also indicating that a shortage of parental provisioning accounted for the difference in mortality.

Lesser black-backed gulls in poor condition have been found to bias the sex ratio of their offspring at hatching towards daughters (Nager et al. 1999). There are three ultimate pressures that favour the evolution of this response: male chicks are more adversely affected than female chicks by poor egg quality (Nager et al. 1999); survival in all-male broods is very low, and female parents in poor condition are less able to rear sons than daughters (this study). While, as we have demonstrated experimentally, such effects can act independently of each other, they will act in concert in natural conditions and need to be considered when formulating our understanding of the evolution of offspring sex ratio. In the wild, parents may be able to ease the detrimental effects of poor condition on breeding success by manipulating the sex ratio of their offspring. Thus, the trade-off between current effort and future fitness as well as the fitness returns through male and female offspring need to be considered in order to understand optimal reproductive strategies.

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