Sex of the first hatched chick influences survival of the brood in the herring gull (*Larus argentatus*)

S.-Y. Kim & P. Monaghan

Division of Environmental and Evolutionary Biology, IBLS, University of Glasgow, Glasgow, UK

Abstract

Differences in the growth rate of male and female offspring can result in different parental rearing costs for sons and daughters. Such differences may also influence the survival chances of male and female offspring when conditions are unfavourable. In birds, hatching asynchrony leads to hierarchical competition for food between siblings. Therefore, the sex of the chick in the first hatched position in the brood may influence breeding success by affecting the extent to which the later hatched chicks can compete for resources. The interaction between brood sex composition and chick performance in the herring gull *Larus argentatus* was examined under different environmental conditions. When environmental conditions were relatively good, chick survival within broods was better when a female was first to hatch, an effect that was most obvious later in the season. When conditions were poorer however, sex of the first hatched chicks was not related to brood survival. In neither situation did the overall primary sex ratio differ from equality. However in the year of relatively good food availability, the first chick in the brood was more likely to be male early in the season, which was when the disadvantageous effects on brood survival of males being in this position are weakest.

Introduction

In long-lived, iteroparous breeders, there is a need to optimize resource allocation across current and future reproductive events. Such strategic decisions may involve offspring sex allocation within and between breeding events, where this influences lifetime reproductive success (Stearns, 1992). Many animal species across diverse taxa show sexual size dimorphism, with differential resource requirements of sons and daughters (Clutton-Brock, 1991). The increased resource requirement of the larger sex may make itself, and possibly also its siblings, more vulnerable to adverse effects of poor food supply during the growth period. Many studies have provided evidence of sex-biased mortality of offspring in species with sexual size dimorphism. When parents are not able to feed their young sufficiently, the more vulnerable sex is usually less likely to grow normally and survive (Silk, 1983; Clutton-Brock, Albon & Guinness, 1985; Cooch *et al.*, 1997; Nager *et al.*, 2000; Daunt *et al.*, 2001; but see Nisbet & Szczys, 2001).

Although there are many reports of sex-biased mortality of offspring in birds, there have been relatively few studies of the effects of brood sex composition on breeding success (but see Nager *et al.*, 2000; Laaksonen *et al.*, 2004). Particularly in species with hatching asynchrony, sex of the chick in the more dominant position in the brood is likely to influence the brood survival rate because of the consequential asymmetric sibling competition (Drummond *et al.*,

1991). When the first hatched chick is the larger sex, this chick is more likely to dominate and outcompete its siblings than when the first hatched chick is the smaller sex.

In herring gulls *Larus argentatus*, the fully grown male is about 20% heavier than the female (Malling-Olsen & Larsson, 2003), and therefore male chicks are likely to be the more expensive sex to rear. Male chicks may be more vulnerable to food-related stress than females because of their faster growth rates (Torres & Drummond, 1997; Velando, 2002). However, little is known about sex differences in growth rate in herring gull chicks, although Griffiths (1992) showed that male chicks grow faster in a closely related species, the lesser black-backed gull *Larus fuscus*. The modal clutch size of the herring gull is three, and chicks hatch asynchronously with the first and second chicks usually hatching 1 day earlier than the third chick (Drent, 1970; Parsons, 1975; Hébert & Barclay, 1986); they are more likely to outcompete the smaller third hatched chick, which has the lowest survival rate (Hillström, Kilpi & Lindström, 2000).

In the present study, we examined the relationship between brood sex composition and chick survival in herring gulls in 2 years that differed in environmental conditions. We examined whether the sex composition of the brood was related to chick survival when conditions were good and when they were poor. We also examined whether the sex composition of broods varied in relation to parental or environmental circumstances.

Methods

We carried out this study from April to July 2002 and 2003 at a mixed colony of herring and lesser black-backed gulls in the South Walney Nature Reserve, Walney Island, Cumbria, UK ($54°08'$N, $03°16'$W). We surveyed the study areas once daily during egg laying, and marked new nests containing an egg with numbered bamboo sticks. We recorded laying dates for 343 nests in 2002 and 266 nests in 2003 in the same study areas, although the areas were slightly reduced in 2003.

We visited each study nest until clutch completion, and marked eggs individually on the day of laying with a permanent marker. We estimated the expected hatching date by adding 29 days to the first egg laying date, and checked each nest daily beginning 2 days before the estimated hatching date until all the chicks were hatched. We marked all chicks using leg flags made with coloured tapes on the day of hatching (day 0) for identification within each brood. We randomly selected a subset of nests hatching three eggs successfully in each year to investigate chick growth and survival (2002, $n = 49$; 2003, $n = 46$). Thus, clutch size and initial brood size were standardized. We visited each nest every 4 days until day 31 to measure the growth and record the survival of chicks. Because chicks become much more mobile and move further from their nest sites as they grow, we were unable to continue the growth measurements after day 31. We weighed chicks to the nearest 0.1 g using an electronic balance when under 200 g, then to the nearest 1 g using spring balances, and measured wing length to the nearest millimetre. We calculated the growth rates in chicks that survived to day 31 over the linear growth phase (Coulson & Thomas, 1985; Wendeln & Becker, 1999), usually beginning from day 3 onward in mass and from day 7 onward in wing length in larids.

To identify the sex of the chicks, we collected a droplet of blood from the leg of each chick on the day of hatching under Home Office licence, using a sterile needle and a capillary tube. This was mixed with an equal volume of BLB buffer, and frozen later the same day. We identified chick sex from blood cell DNA, using two CHD genes (Griffiths, Dann & Dijkstra, 1996). The samples were sexed only where all three chicks had been sampled in the complete brood. Therefore, the brood sex ratio at hatching was the same as the primary sex ratio at laying. We identified the sex composition of 49 broods in 2002 and 118 broods in 2003.

The adult birds in our study areas were mostly unmarked. However, because herring gulls show strong breeding site fidelity and relatively low adult mortality, many of the study birds will be the same across years; therefore, we analysed each year separately to avoid non-independence in the analyses. We examined factors influencing linear growth rates of mass and wing length using separate statistical models for each year. We used generalized linear mixed effect models (GLMMs) incorporating nest identity as a random effect to account for the non-independence of chicks from the same brood (Crawley, 2003). We examined brood survival rate (proportion of the brood surviving until day 31) in separate generalized linear models (GLMs) with a binomial error distribution and a logit link. Models initially included all explanatory variables and two-way interactions. Final models were selected by sequentially dropping non-significant interactions and then non-significant main effects (Crawley, 2003). The results of model fittings are presented for all main effects and significant interactions. We examined the primary sex ratio of offspring in each laying position and the effect of laying date using binomial test and binary logistic regression. Data were analysed using R v1.8.0 (2003) and SPSS v10.0 (1999).

Results

Differences in laying date and breeding success between years

The distributions of laying dates in herring gulls did not differ from normal in either 2002 or 2003 (Kolmogorov–Smirnov test: 2002: $Z = 1.21$, $n = 343$, $P = 0.11$; 2003: $Z = 1.01$, $n = 266$, $P = 0.26$). Overall, egg laying was around a week later in 2003 compared with 2002 (mean laying dates expressed as number of days from 1 April $\pm$ SE; 2002: 32.99 ± 0.30; 2003: 39.54 ± 0.31; $t_{608} = -14.95$, $P < 0.001$). Chicks in 2003 were fed less frequently than those in 2002, and also the different diet composition of chicks between years suggested that the quality of food was higher in 2002 (Kim, 2005). The overall breeding success of pairs laying three egg clutches was significantly higher in 2002 than in 2003 (mean number of chicks survived until day 31 per nest $\pm$ SE: 2002: 2.20 ± 0.15, $n = 49$; 2003: 1.43 ± 0.18, $n = 46$; Mann–Whitney test: $U = 716.00$, $P = 0.001$). Conditions during the breeding season thus appeared better in 2002 than in 2003.
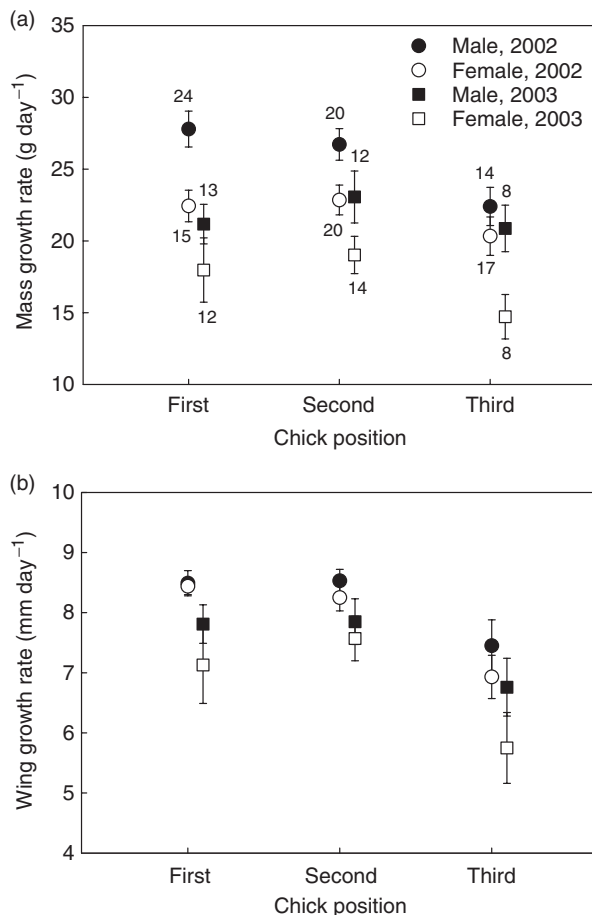
Chick growth and survival

Laying date, sex of the first chick and number of males in the brood were not related to the growth of chicks in any consistent way in either year (Table 1). However, as is generally the case, the growth rates of mass and wing length were significantly related to the position of the chick in the brood in both years (Table 1). In general, the first and second chicks grew faster than the third chicks (Fig. 1a and b). Male chicks grew significantly faster than females in mass in both years, independent of their position in the brood (Fig. 1a; Table 1). However, although the pattern was similar for wing length, there was no significant sex difference in either year (Fig. 1b; Table 1). Overall, chicks grew faster in 2002 than in 2003 (GLMM: wing length: likelihood ratio $= 7.865$, d.f. $= 1$, $P = 0.005$; mass: likelihood ratio $= 13.128$, d.f. $= 1$, $P < 0.001$; Fig. 1).

The number of male chicks in the brood did not influence the brood survival rate (proportion of brood surviving until day 31) in either year (Table 2). In 2002, which is the year of higher breeding performance, the brood survival rate was higher when a female chick was in the first hatching position (mean proportion of chicks surviving per brood $\pm$ SE:

Table 1 Summary of GLMMs examining the effects of sex of the first chick (Asex), number of male chicks (nomale) in the brood, position and sex of chick, and laying date (laydate) on linear growth rates of chicks in (a) 2002 and (b) 2003 (random effect: nest identity)

	Wing length			Mass		
Variable	L. ratio	d.f.	P	L. ratio	d.f.	P
(a) 2002						
Asex	0.001	1	0.981	0.171	1	0.679
Nomale	1.014	1	0.314	0.083	1	0.774
Position	41.776	2	0.000	22.135	2	0.000
Sex	0.363	1	0.547	30.781	1	0.000
Laydate	2.879	1	0.090	2.192	1	0.139
(b) 2003						
Asex	0.101	1	0.751	1.249	1	0.264
Nomale	0.618	1	0.432	1.011	1	0.915
Position	24.763	2	0.000	7.964	2	0.019
Sex	0.826	1	0.363	10.855	1	0.001
Laydate	3.137	1	0.077	2.601	1	0.107

The significance reported is the likelihood ratio (L. ratio) when the explanatory variable of interest is dropped from the model; unless otherwise stated, interactions were not significant.
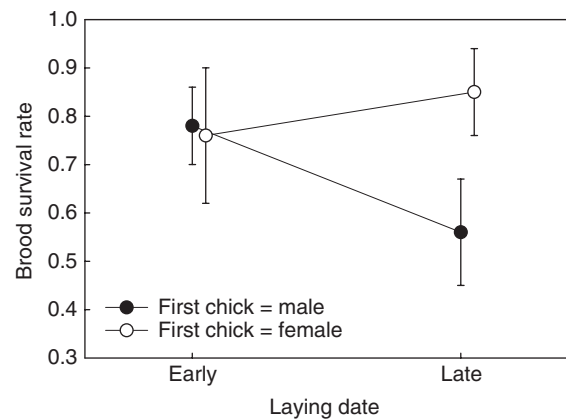GLMM, generalized linear mixed effect model.

Table 2 Summary of GLM with a binomial error distribution and a logit link examining the effects of sex of the first chick (Asex), number of male chicks (nomale) in the brood and laying date (laydate) on brood survival rate (proportion of chicks surviving per brood until day 31) in (a) 2002 and (b) 2003

Variable	F	d.f.	P
(a) 2002			
Asex	4.017	1	0.045
Nomale	0.441	1	0.507
Laydate	1.563	1	0.211
Asex : laydate	4.106	1	0.043
(b) 2003			
Asex	0.672	1	0.412
Nomale	2.394	1	0.122
Laydate	1.590	1	0.207
Asex : laydate	0.089	1	0.766

The significance reported is the F value when the explanatory variable of interest is dropped from the model; unless otherwise stated, interactions were not significant.
GLM, generalized linear model.

Figure 1 Linear growth rates (means ± SE) of (a) mass and (b) wing length according to position and sex of chicks.


Figure 2 Comparison of brood survival rate (proportion of brood surviving until day 31) between nests with male and female chicks in the first hatching position based on laying date (early: 23–30 April; late: 1–10 May) in 2002.

0.81 ± 0.08, $n = 18$) than when a male was first to hatch in the brood (0.69 ± 0.07, $n = 31$). Interestingly, the interaction between sex of the first chick and laying date was also significant, suggesting that the relationship between brood survival and laying date differed between nests with different sexes in the first position (Table 2). Early (i.e. before the median laying date) in the season, sex of the first chick seems to have little effect on brood survival; later in the season (i.e. after the median laying date), survival in broods with a male in the first position dropped substantially, whereas survival in broods with a female in the first position increased very slightly (Fig. 2). In 2003, the sex of the first chick did not influence brood survival (mean proportion of chicks surviving per brood ± SE: first chick = male: 0.51 ± 0.10, $n = 21$; first chick = female: 0.45 ± 0.07, $n = 25$; Table 2).

Table 3 Primary sex ratio of offspring in each laying position in the clutch (or brood) in (a) 2002 ($n = 49$ broods) and (b) 2003 ($n = 118$ broods)

Chick position	Male (%)	Female (%)	Binomial test P	Logistic regression X_1^2	P
(a) 2002					
First	63.3	36.7	0.085	4.332	0.037
Second	51.0	49.0	1.000	0.600	0.439
Third	46.9	53.1	0.775	0.622	0.430
(b) 2003					
First	43.2	56.8	0.167	0.472	0.492
Second	52.5	47.5	0.646	0.056	0.813
Third	44.9	55.1	0.311	5.081	0.024

The statistics are from a binomial test of sex ratios to examine if they differ from equality, and binary logistic regression to examine the relationship between sex and laying date.
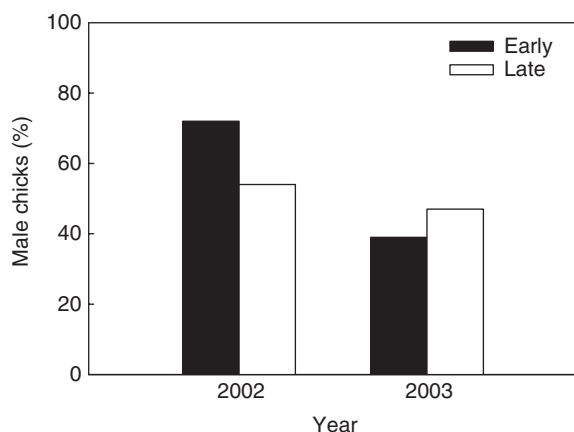
Figure 3 Percentage of male chicks in the first hatching position in 2002 (early: 23–30 April; late: 1–10 May) and 2003 (early: 1–9 May; late: 10–19 May) based on laying date.

Primary sex ratio

In neither year did the overall primary sex ratio differ significantly from equality for chicks from either the first, second or third laid eggs (Table 3). However, logistic regression models suggested that in 2002 the first hatched chicks were male biased early in the season, but this disappeared later (binomial test: early: $P = 0.043$, late: $P = 0.84$; Table 3; Fig. 3), whereas there was no seasonal effect on sex of the first hatched chicks in 2003 (early: $P = 0.118$, late: $P = 0.795$; Fig. 3; Table 3).

Discussion

Chick growth varied with respect to both sex and position in the brood. Male chicks gained body mass faster than females. Such sex differences in juvenile growth can result in differences in the costs of rearing sons and daughters because of their different food requirements (Clutton-

Brock, 1991). Also, the first and second chicks grew faster than the third chicks, presumably because of their competitive advantages conferred by being larger and hatching earlier (Hillström *et al.*, 2000). When a male chick has the additional advantage of hatching first, its increased competitive ability coupled with higher food requirements may negatively influence the overall breeding success of the brood under some circumstances (Drummond *et al.*, 1991).

At our study colony, there was a difference in food availability between 2002 and 2003, as evidenced by the timing of breeding being delayed in 2003, and the reduced growth and survival of chicks compared with 2002. In herring gulls, the probability of rearing three chicks in the brood is generally low unless environmental circumstances are particularly good. More typically, only one and sometimes two chicks are reared. Where conditions are very good, having a female in the first position may increase the probability of more than one chick surviving. In 2002, the average breeding success among pairs having three chicks was 2.20 ± 0.15 chicks per nest. In this year overall, broods with a female in the first position were most successful, independent of the laying date. Interestingly, chick survival in broods with a male in the first position decreased late in the season, whereas it increased very slightly in broods with a female in the first position. It may be that having a more expensive sex in the first position is disadvantageous for later, probably younger (Coulson & White, 1958; Davis, 1975; Sæther, 1990), breeding pairs.

Many studies have shown that sex of the chick can directly influence its survival in species with sexual size dimorphism because the larger sex requires more resources (Griffiths, 1992; Kalmbach *et al.*, 2001) or is more vulnerable because of its faster growth rate (Torres & Drummond, 1997; Velando, 2002). However, the survival of a chick may also be influenced by the sex of its siblings, particularly when they are in unequal competitive positions in the brood during the early growth period because of their hatching asynchrony (Drummond *et al.*, 1991; Bradbury & Griffiths, 1999; Nager *et al.*, 2000). Because male chicks demand more resources during the nestling period and the first hatched chicks usually dominate their siblings in the herring gull, sex of the chick in the first position may be important for the survival of the brood. Nager *et al.* (2000) found that prefledging survival of male chicks was strongly reduced in all-male broods whereas female chicks were unaffected by brood sex composition in a closely related species, the lesser black-backed gull. In the year when conditions were not quite so good however, there was no evidence that the sex of the first chick influenced overall breeding success in the present study.

Trivers & Willard (1973) argued that selection should favour parental ability to tailor offspring sex ratio within and between breeding events to parental investment capability and/or environmental conditions influencing the reproductive value of male and female offspring. Parents may gain higher fitness by skewing sex ratio of offspring towards the sex that is more likely to survive in the prevailing environmental circumstances (Ryder, 1983). There is

now growing evidence that food availability influences laying sex ratio in birds (Nager *et al.*, 1999; Arnold *et al.*, 2003; Rutstein, Slater & Graves, 2004). In the present study, neither year showed significant inequality of sex ratio in the herring gull. However in 2002, the probability of male chicks hatching from the first laid egg in the clutch was highest early in the breeding season, which was when having a first hatched male chick did not confer any disadvantage. Seasonal changes in offspring sex according to the laying sequence have also been shown in other studies (Velando, Graves & Ortega-Ruano, 2002; Genovart *et al.*, 2003). As sex of the first hatched chick and its interaction with laying date are important factors influencing breeding success in the herring gull as explained above, parent birds may allocate sex of the first laid egg in relation to their rearing capacity or the environmental conditions within the breeding season. This is most likely linked to maternal condition, which is known to affect laying sex ratio in gulls (Nager *et al.*, 1999). Therefore, poor-quality birds who breed later in the season may be less likely to produce male eggs in the first position in the clutch. It has been argued that particular sex combinations in a brood should be favoured over more vulnerable combinations that are associated with reduced chick survival (Cockburn, Legge & Double, 2002), which will of course depend on parental provisioning capacity. Facultative adjustment of laying sex ratio in birds needs more experimental investigation because the mechanisms are currently unknown and results are patchy (Krackow, 1995).

Acknowledgements

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