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ORIGINAL ARTICLE

Consequences of sex-specific growth on sibling competition in black-headed gulls: a sexually-size dimorphic species with scramble competition

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Abstract Biased mortality of the larger sex during the early developmental period has been reported for a number of size-dimorphic bird species. This can partly be explained by the fact that growing to larger size renders the larger sex more vulnerable to food shortage. However, since sibling rivalry is often size-dependent, chicks of the larger sex should have a competitive advantage. This raises the question as to why the larger sex does not always benefit from its size in sibling competition. We studied sibling competition in the black-headed gull (*Larus ridibundus*), a sexually-size dimorphic species with male-biased mortality. We manipulated the natural brood sex ratio and placed one male chick in direct competition with one female chick while concurrently controlling for differences in age, size and laying order. Male chicks outgrew their female siblings by 15% in asymptotic body mass and did not suffer from enhanced mortality. Female chicks tended to be more alert when the parents returned to the nest and were more persistent in gull-typical begging displays. Females were more likely to get the first food item, but they did not get more food, possibly due to a size-mediated dominance over the non-monopolizable regurgitated food. Thus, it is unlikely that sex differences in competitiveness significantly contribute to male-biased mortality in black-headed gulls. The previously reported male-biased mortality is more likely due to a disadvantage of a higher food demand and a higher sensitivity towards low egg quality, as has been shown in previous studies.

Keywords Begging · Egg quality · Growth rate · Hatching asynchrony · Sex ratio

Introduction

Starvation-mediated mortality as a function of sibling competition represents a major cause of death for developing offspring in birds (Lack 1954). The smallest (often youngest) individuals within a brood generally have a competitive disadvantage and are, therefore, less likely to survive. This pattern is particularly expressed in species that hatch their chicks asynchronously (e.g. O'Connor 1978; Mock et al. 1990). In addition to hatching order-dependent size differences, siblings may also differ in size due to sex-specific growth patterns, such as those that occur in sexually dimorphic species (Badyaev 2002). However, in sexually dimorphic species, it is often the larger sex that suffers from enhanced mortality (Clutton-Brock et al. 1985; Røskraft and Slagsvold 1985; Griffiths 1992; Torres and Drummond 1997). It has been suggested that higher energetic requirements of the larger sex (Anderson et al. 1993a; Krijgsveld et al. 1998; Riedstra et al. 1998; Vedder et al. 2005) may render it more vulnerable to periods of food shortage (Røskraft and Slagsvold 1985; Nager et al. 2000). While this may explain the mortality pattern in dimorphic species with single offspring, it raises the question as to why individuals of the larger sex do not benefit from their larger size under conditions of sibling competition in those cases where the

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brood contains members of both sexes. In some species, the larger sex indeed seems to have a competitive advantage, as suggested by the higher survival probability of the larger sex, which is in contrast to the observed mortality patterns described above (Anderson et al. 1993b; Arroyo 2002; Hipkiss et al. 2002). This difference between species in terms of enhanced mortality of the smaller or, respectively, larger sex has recently been suggested to depend on the brood size and the importance of a size-dependent dominance (Råberg et al. 2005)—i.e. better competitive skills of the larger sex outweigh the physiological disadvantage of a higher food demand in large broods, rendering the smaller sex more sensitive (Anderson et al. 1993a).

However, to what extent sex differences in begging behaviour/competitiveness contribute to sex-biased mortality is yet unclear (Mock and Parker 1997). There are two studies reporting on sex differences in begging and survival within the same species. In the red-winged blackbird (*Agelaius phoeniceus*), the larger males suffer from enhanced mortality (Blank and Nolan 1983), even though they are dominant in terms of sibling competition (Teather 1992). In contrast, the larger females dominate the smaller males in the reversed sexually dimorphic American kestrel (*Falco sparverius*), and mortality is accordingly male-biased [Anderson et al. 1993b; see also Fargallo et al. 2003 for the European kestrel (*Falco tinnunculus*)]. This indicates that different processes may be involved in sex-biased mortality and that it is important to disentangle those processes by taking different measures of sibling competition into account (Clutton-Brock 1991).

Sex differences in mortality also depend on factors such as the degree of hatching asynchrony, since the larger sex suffers heavier mortality if hatched late—that is, when it is placed under a condition of competitive disadvantage (Dzus et al. 1996; Torres and Drummond 1997; Bradbury and Griffiths 1999). However, other factors may also play a role, and chicks hatching comparatively late in the sequence are not only handicapped by an age difference, they often hatch from eggs of lower quality (for example, in terms of contents of carotenoids or antibodies; in gulls, see Royle et al. 1999; Blount et al. 2002; Groothuis et al. 2006). Enhanced mortality among the larger sex may therefore also result from the reported higher sensitivity of the larger sex to changes in egg quality (Nager et al. 1999; Müller et al. 2005a). Thus, the lower survival of later hatched offspring of the larger sex is not necessarily only due to a competitive disadvantage in sibling rivalry based on developmental status.

In the investigation reported here, we focused on the role of sex differences in competitiveness while controlling for as many other variables as possible. We manipulated the natural brood sex ratio and placed a male and a female black-headed gull chick (*Larus ridibundus*) in a direct competitive situation, while at the same time we controlled for age, size and egg quality differences. Black-headed gull males are about 15% heavier and skeletally larger than females (Glutz von Blotzheim and Bauer 1982) and suffer from enhanced mortality (Müller et al. 2005a, b; see also Sayce and Hunt 1987; Griffiths 1992; Nager et al. 2000 for other gull species). The black-headed gull is particularly appropriate this type of study because the chicks directly compete for food that the parents regurgitate on the ground. The likelihood of obtaining food in the scramble competition is subsequently dependent on the competitive skills of a chick rather than on parental feeding preferences, while no directed aggression can be observed.

If, as has been reported for this species, the biased mortality is affected by sex differences in competitiveness, we would expect that males should be disadvantaged in sibling competition.

Materials and methods

Study population

Fieldwork was conducted during 2001 on two black-headed gull colonies (colony 1: about 2000 breeding pairs; colony 2: about 300 pairs), both situated at locations along the northeast coast of The Netherlands. In colony 1, eggs were marked with a non-toxic marker to record the position in the laying order and date that they were laid. Shortly before hatching [3 days ± 0.08 SE], 315 eggs of known laying date and laying position were taken to the incubator at the University of Groningen to perform two experiments, one of which is reported here (see also Müller et al. 2005a). Within 2–3 h after hatching, the chicks were weighed to the nearest 0.1 g and marked with a small numbered plastic band for individual identification. A small amount of blood (20 µl) was taken for molecular sex determination by puncturing the ulnar vein (Griffiths et al. 1998). Due to adverse weather conditions and the consequent total loss of colony 1 during the beginning of our experiment, we were unable to place the chicks in natural foster broods at the day of hatching. Therefore, the chicks were housed in groups of similar age util they were maximally 5 days old. During this time, they were ad lib hand-fed with fresh fish three times a day until they were moved to colony 2. On the day of fostering we then composed broods of one male and one female chick (average natural brood size, since the last-hatched chicks typically dies within the first few days) that had been matched for laying position, body mass of that day and age ($N = 20$ nests).

We subsequently increased the number of experimental nests by using hatchlings that were born in colony 2 during the period of behavioural observations. These chicks hatched in the field, were sexed within 48 h and cross-fostered when about 3 days old. As for colony 1, these nests were matched for age, hatching position and body mass, containing one male and one female chick (*N* = 13 nests). Laying order was not known in colony 2. We therefore only used chicks of nests that hatched three chicks (natural clutch size) asynchronously to assure that hatching order corresponded with laying order (Müller et al. 2003).

Experimental broods

Experimental broods were selected 1 day in advance of the actual cross-fostering and were temporarily (3–4 days) placed in small enclosures (1 m^2 surrounded with opaque mesh) to prevent the chicks from moving to neighbouring nests before the adoption was established. These small enclosures were situated within four larger enclosures (wire mesh, 40–50 cm high) of about 25 m^2 (for details on methodology, see Müller et al. 2005a). The large enclosures contained 5–15 experimental nests and enabled us to follow chick development and begging behaviour until the time of fledging. To maximize adoption rate, we selected nests that contained chicks of the same age as the foster chicks. The original chicks were placed in neighbouring incomplete broods of chicks of the same age.

Nine nests had to be excluded due to logistic reasons and/or mortality of at least one chick within 1 day after cross-fostering. In the case of the latter, we can not exclude that this is related to the adoption procedure, and these nests are therefore not included in any further analysis. In the remaining 24 experimental nests, there was no significant difference in weight at hatching [males: 27.53 (±SE) ± 0.53 g, *N* = 24; females: 28.04 ± 0.78 g, *N* = 24; paired *t*-test, *t* = –0.56, *p* = 0.58) or at cross-fostering (males: 42.18 ± 2.30 g, *N* = 24; females: 40.37 ± 2.32 g, *N* = 24; paired *t*-test, *t* = 1.67, *p* = 0.11]. Age at cross-fostering was 3.33 ± 0.33 days in males (*N* = 24) and 3.25 ± 0.31 days in females (*N* = 24) (paired *t*-test, *t* = 1.44, *p* = 0.16). Ten nests were composed from chicks hatching from first-laid eggs, seven from second-laid eggs and seven from last-laid eggs.

Behavioural observations

We recorded chick behaviour using Canon vision EX1 cameras with a 120-mm zoom lens from hides placed on elevated platforms 2–3 m away from the enclosures. At the end of the field season, the tapes were scored in the laboratory by an observer unaware of the chick's sex. The chicks were randomly coloured in green or red on the head, chest and/or wings for individual recognition from a distance. Recordings of the begging behaviour started when the chicks were about 13 days old and continued as long as the nest contained two experimental chicks. Each enclosure was observed daily in random order for 1.5 h, either in the morning between 08.00 and 11.00 a.m. or between 13.00 and 16.00 p.m.

Black-headed gull chicks show conspicuous begging behaviours to stimulate parents to feed by means of regurgitating food onto the ground. These behaviours were scored as described in Eising and Groothuis (2003). Briefly, a begging bout was started with the first reaction of a chick to a parent and ended when no chick was showing any sign of begging for at least 10 s. Typical begging displays consist of up and down head movements and hunched postures ('pumping') accompanied by a call during the downward movement and pecking at the bill of the parent ('bill-pecking'). The frequency of these behaviours was recorded. As a measure of alertness, we scored which chick was the first to respond to the parent's return, to approach the parent and to show 'pumping' or 'bill-pecking' behaviour. When parents regurgitated food, we scored which chick was the first to eat and, if the food items could be quantified, which chick obtained the largest proportion of food. Since not all behaviours were observed in all nests, sample sizes may differ for each of the behaviours scored, as indicated in the Results by the given degrees of freedom. In the absence of their parents, chicks defend the territory against intruding neighbours, both chicks and adults. These between-nest interactions were recorded throughout the observation periods, since it has been suggested that hungrier chicks are more active and more likely to suffer from (lethal) interactions with neighbours (Hunt and Hunt 1976).

In total, we were able to record begging behaviour in 16 nests. We observed on average 72 feeding bouts per nest during (on average) 13 different days.

Growth and survival

We measured body mass (to the nearest 0.5 g using a Pesola spring balance) and tarsus and head-bill length (both to the nearest 0.1 mm using a caliper) of all chicks every third day. Nests were removed from the analysis when one of the chicks died or fledged. Fledgling age was defined as the last day that a chick was observed within its enclosure.

Statistical analyses

Growth (body mass gain and skeletal growth) was analysed using hierarchical linear models in the MLwiN programme ver. 1.10 (Bryk and Raudenbush 1993; Rasbash et al. 2000). This method accommodates unbalanced data and allows analyses of variances and co-variances taking the nested relationship of different chicks in a nest into consideration as well as controlling for multiple (independent) variables. Data were analysed in a three-level model: nest (first level), individual (second level) and repeated measures within the individual (third level) (see also Eising et al. 2001; von Engelhardt et al. 2005). To model the sigmoidal growth curve, we included age, age^2 and age^3 as predictors in the model analysing offspring mass and size. The following variables were included in the analysis: sex, laying position (categorical variable), hatching date and all possible interactions. Significance was tested using the increase in deviance when a factor was removed from the model that follows a χ^2-distribution (Wald statistic). We included only data in the analysis that were obtained after cross-fostering, with the exception of hatching mass and size, which were included for an optimal growth fit.

Survival data were analyzed using the life-tables option in SPSS (SPSS, Chicago, Ill.). The differences in average pumping or bill pecking frequency per feeding bout between the sexes were tested using a paired-sample *T*-test. Alertness scores—the proportion of bouts a chick was the first to react, to approach, to pump, to peck or to eat—was averaged over all begging bouts. The proportions, which are complementary for the two chicks in the nest, were arcsin transformed and analysed using a one-sample *T*-test to see whether the proportion deviated significantly from 50%. Sex differences in the total number of territorial interactions were analysed using Wilcoxon signed rank test.

Results

Behaviour

Sex differences in begging behaviour are illustrated in Fig. 1. Time of the day did not affect feeding rates or (sex) differences in begging behaviour and is therefore not included in the following analyses.

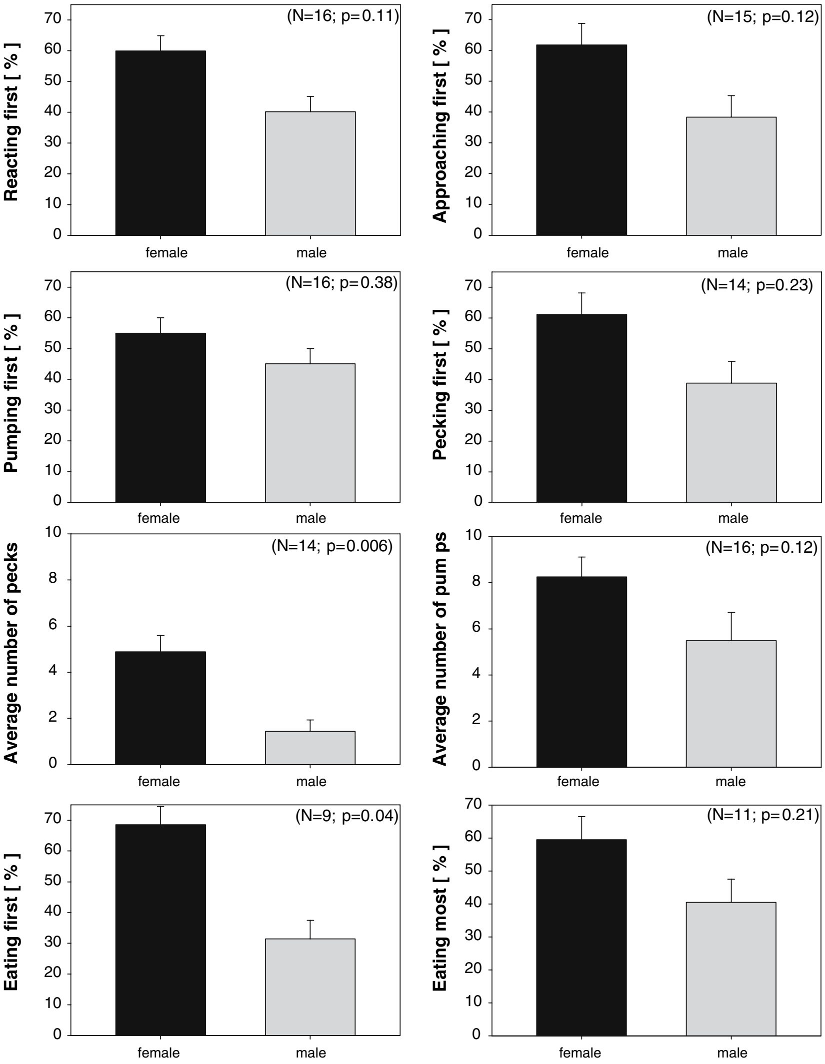

Fig. 1 Begging behaviour of male (*black bars*) and female (*white bars*) black-headed gull chicks (mean ± SE): proportion of being the first to react to an approaching parent, proportion of being the first to actively approach the parent, proportion of pumping first or to start pecking at the parent's bill first, average number of pumps and average number of pecks at the parent's bill per begging bout and proportion for eating first and most

Female chicks were more often the first to react to a returning parent as well as to approach the parent, although this was not statistically significant (first react one-sample *T*-test $t_{15} = -1.70$, $p = 0.11$, $N = 16$; first approach: one-sample *T*-test $t_{14} = -1.66$, $p = 0.12$, $N = 15$).

There was no sex difference in the likelihood to be first to display either 'pumping' or 'bill pecking' behaviour (first pump one-sample *T*-test $t_{15} = -0.90$, $p = 0.38$, $N = 16$; first peck: one-sample *T*-test $t_{13} = -1.25$, $p = 0.23$, $N = 14$). Female chicks pumped on average more often per feeding bout than male chicks, but not significantly so (paired *T*-test $t_{15} = -2.77$, $p = 0.12$, $N = 16$), and they pecked significantly more often towards the bill of the parent compared to male chicks (paired *T*-test $t_{15} = -3.28$, $p = 0.006$, $N = 14$).

Female chicks were more often the first to start eating when the parents had regurgitated food (one-sample *T*-test $t_8 = -2.40$, $p = 0.04$, $N = 9$) (Fig. 1). There was no sex difference in the amount of food a chick could eat (one-sample *T*-test $t_{10} = -1.35$, $p = 0.21$, $N = 11$) (Fig. 1). However, this could only be scored if food items such as fish were delivered that could be monopolized. This was the case in less than 30% of the feeding bouts.

Aggressive territorial interactions could be observed in 16 nests. Males ($N = 16$) defended the territory against intruding chicks or adults on average 6.5 ± 2.5 times, females ($N = 16$) on average 5.3 ± 1.5 times (Wilcoxon signed ranks test, $z = -0.85$, $p = 0.40$). There was no sex difference in how often male or female chicks were attacked by intruders (males 3.6 ± 1.14, $N = 16$; females 3.0 ± 0.98, $N = 16$; Wilcoxon signed ranks test, $z = -0.35$, $p = 0.74$).

Growth

Body mass gain

In the analysis on body mass, age, age^2 and age^3 revealed significant effects reflecting growth (Δdev > 16.79, $df = 1$, $p < 0.0001$ in all cases). There was a significant positive effect of the interaction of sex and age (estimate of 0.95 error: 0.19, Δdev = 25.19, $p < 0.0001$), with males gaining significantly more weight than females (Fig. 2). Body mass was not influenced by the position in the laying order (Δdev = 1.52, $df = 2$, $p = 0.47$), but there was a tendency for an effect of laying position in interaction with age and sex (laying position × age × sex: Δdev = 4.61, $df = 2$, $p = 0.10$).

Logistic growth curves were fitted for males and females respectively using least squares regression (SPSS ver. 12.0) using the model: $W = A/(1 + e^{-k*(t - t_I)})$, in which W is body mass at a given age, A is asymptotic body mass (g), k (day^{-1}) is the logistic growth constant (Ricklefs 1968), and t_I is the point of inflection (day). Asymptotic body mass was 268.09 (g) for males and 232.51 (g) for females. Thus, the sexual size dimorphism in asymptotic body mass was 15%. The logistic growth constant k was 0.18 for male chicks and 0.19 for female chicks. Males reached the inflection point t_I when 11.56 days old, females when 11.24 days old.

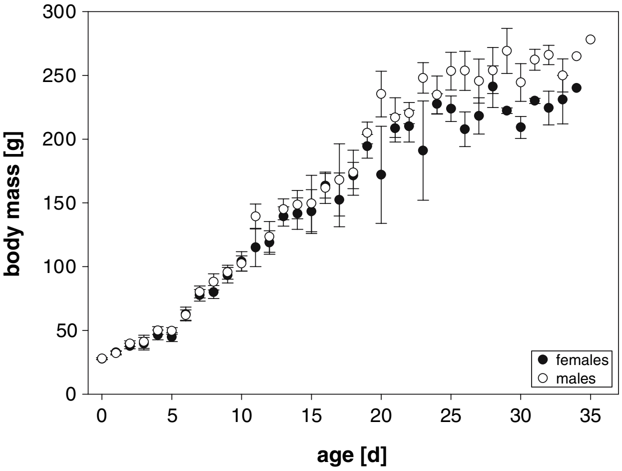

Fig. 2 Mean body mass (g) in relation to age (day, *d*) of male (*open circles*, $N = 24$) and female black-headed gull chicks (*filled circles*, $N = 24$). *Bars*: standard error

Skeletal growth

There was a significant effect of age and age^2 on head-bill and tarsus length, reflecting growth (Δdev > 239.67, $df = 1$, $p < 0.0001$ in all cases), and a significant positive effect of the interaction of sex and age on both head-bill and tarsus length, with again males showing enhanced skeletal growth compared to females (head bill length: estimate 0.10 error: 0.02, Δdev = 55.26, $p < 0.0001$; tarsus length: estimate 0.07 error: 0.02, Δdev = 15.96, $p < 0.0001$). Laying position in interaction with age had a significant negative effect on head-bill length (Δdev = 15.47, $df = 2$, $p < 0.001$) and tended to have similar effects on tarsus length (Δdev = 5.16, $df = 2$, $p = 0.08$). Skeletal size was not affected by the position in the laying order in an interaction with age and sex (laying position × age × sex: Δdev > 2.48, $df = 2$, $p > 0.29$ in both cases).

Survival

Nine female and nine male chicks died before fledgling. Thus, the probability of survival was not statistically different between the sexes (Wilcoxon Gehan statistic: 0.19, $p = 0.66$), and it was not dependent on the hatching position (Wilcoxon Gehan statistic: 1.57, $p = 0.46$). In the remaining 15 nests that did not show any mortality, we compared the age at fledgling between male and female nest mates. Males ($N = 15$) fledged when an average of 32.07 ± 0.61 days old, females ($N = 15$) when an average of 30.47 ± 0.96 days old. This difference approached statistical significance (paired *t*-test, $t_{14} = -1.88$, $p = 0.08$).

Discussion

The aim of our study was to investigate whether sex differences in begging behaviour contribute to the previously reported male-biased mortality in black-headed gulls. To this end, we experimentally created mixed sex broods while controlling for age, size and laying order.

Males outgrew their female siblings by 15% in asymptotic body mass (Fig. 2), which is somewhat greater than that observed under natural conditions (Müller et al. 2005a). Males did not suffer from enhanced mortality, as has been reported previously for this species (Müller et al. 2005a, b). Female chicks tended to be more alert when the parents returned to the nest with food (Fig. 1) and also to be significantly more persistent in pecking towards the bill of the parent (Fig. 1), which is a basic gull chick behaviour aimed at stimulating the parents to feed (Henderson 1975; Iacovides and Evans 1998). The enhanced begging vigour in females indicates that females are not as successful in meeting their (smaller) needs as males (Henderson 1975; Iacovides and Evans 1998; Kitaysky et al. 2003), since bill-pecking behaviour, for example, which was enhanced in females, has been shown to increase with hunger in Glaucous-winged gulls (*L. glaucescens*) and Ring-billed gulls (*L. delawarensis*) (Henderson 1975; Iacovides and Evans 1998). Furthermore, the tendency of female chicks to be more alert could be explained by the fact that hungrier chicks are thought to be more active (e.g. Hunt and Hunt 1976). In larger gull species, such a higher activity of hungry chicks often leads to severe mortal attacks by adult neighbours (e.g. Hunt and Hunt 1976). However, for our study species, we could not find any evidence that female chicks were more often attacked by neighbours or more often involved in territorial interactions.

Although female chicks were more likely to obtain the first food item, this did not increase their likelihood to obtain more food (Fig. 1). This may be due to the fact that parents mostly delivered non-monopolizable food (in more than 70% of the feeding bouts). Males, although approaching the parent somewhat later, apparently gain an advantage in the competition for food once it is regurgitated. This advantage most probably relates to their larger size and may allow males to invest less in begging displays while still receiving a greater amount of food than its siblings, as predicted by the 'sibling-competition model' (Rodriguez-Girones 1999; Rodriguez-Girones et al. 2001).

The fact that females did not receive more food even though they were the first at the parent is in contrast to a related species, the common tern *Sterna hirundo*, where single and/or monopolizable food items are delivered and, consequently, the ability to reach the parent first increases the likelihood of receiving food (Smith et al. 2005). Thus, not only behavioural differences but also the food type has to be taken into account when determining the outcome of sibling competition. Given the biology of this species, it is unlikely that the food type for our population is different from that of other populations of black-headed gulls (personal observations of authors; Glutz von Blotzheim and Bauer 1982). Our results therefore likely reflect a common situation in black-headed gulls. However, the food conditions were probably good, as indicated by the comparatively high asymptotic body mass (see Müller et al. 2005a for a comparison between different years), which has to be taken into account when analysing the results.

Females may partly be able to compensate for the size disadvantage through their slightly enhanced alertness (potentially as a consequence of their higher hunger level). Alternatively—or in addition—the slightly higher alertness in females may also relate to an earlier maturation of the motor co-ordination of the smaller females, which may increase mobility (Richter 1983). Males may increase weight more rapidly and put relatively more energy to growth in size, but they may remain rather immobile. The hypothesis that the (smaller) females are ahead in the maturation of their motor co-ordination is supported by the tendency of earlier fledgling compared with their male siblings (see also Richter 1983). However, the latter behaviour may also represent a female strategy to escape further competition for food when having a male sibling.

Our results render it unlikely that a competitive disadvantage of male chicks contributes significantly to the previously observed male-biased mortality in gulls. This is in line with the outcome of a previous study suggesting that female chicks potentially suffer from the presence of male chicks (Müller et al. 2005a). In this previous study, male survival was reduced in all-male nests where male chicks did not have female siblings to dominate. This increased mortality was likely a consequence of the higher energetic requirements of male offspring and the higher probability that the parental feeding did not match the food demand of the brood (Nager et al. 2000; Müller et al. 2005a). In contrast to previous studies, we did not find strong evidence that male chicks suffered from lower egg quality (Nager et al. 1999; Müller et al. 2005a). Chicks hatching from eggs laid later in the laying sequence reached similar a body mass but not a similar skeletal size as first-hatched chicks. However, this was not different for the sexes and was potentially due to the dominance of male chicks in sibling competition that allowed them to compensate for their greater sensitivity to low egg quality (Nager et al. 1999; Müller et al. 2005a). The proximate mechanism of the latter is yet unknown, and further studies are needed to unravel the intrinsic differences between males and females in different species (Müller et al 2005b; DeKogel 1997; Martins 2004).

In conclusion, male black-headed gull chicks did not suffer from a competitive disadvantage, and their previously reported increased nestling mortality is probably largely a consequence of their higher energetic requirements and an enhanced sensitivity to low egg quality (Nager et al. 1999, 2000; Müller et al. 2005a). The fact that female chicks were slightly more alert and more persistent in begging is likely explained by their greater hunger. The outcome of this study does not support the hypothesis from Råberg et al. (2005) arguing that small brood sizes would offset the size-advantage in sibling competition.

Zusammenfassung

Konsequenzen von geschlechtsspezifischen Wachstumsunterschieden auf die Nestlingskonkurrenz—eine experimentelle Studie bei Lachmöwen

Bei geschlechtsdimorphen Arten haben die Nachkommen des grösseren Geschlechts oft eine schlechtere Überlebensrate während der frühen Entwicklungsphase. Dies wird zum Teil dadurch erklärt, dass der mit dem verstärkten Wachstum verbundene grössere Futterbedarf das Risiko erhöht, während einer Periode mit schlechten Nahrungsbedingungen zu sterben. Allerdings haben grössere Individuen im Allgemeinen oft einen Vorteil in der Nestlingskonkurrenz, so dass das grössere Geschlecht eigentlich einen Vorteil in der Nestlingskonkurrenz haben sollte, was allerdings nicht immer der Fall ist. Um dies genauer zu studieren, haben wir bei Lachmöwen (*Larus ridibundus*), einer geschlechtsdimorphen Art mit erhöhter Sterblichkeit der (grösseren) männlichen Küken, die Nestlingskonkurrenz untersucht. Wir haben dazu das Geschlechterverhältnis in natürlichen Bruten manipuliert, und ein männliches in direkte Konkurrenz zu einem weiblichen Küken gesetzt, wobei wir für Alter, Grösse und Gelegefolge korrigiert haben. Männliche Küken erreichten ein 15% schwereres asymptotisches Gewicht verglichen mit weiblichen Küken und zeigten keine erhöhte Sterblichkeit. Weibliche Küken reagierten schneller auf die zum Nest zurückkehrenden Alttiere und waren ausdauernder in den für Möwen typischen Betteldisplays. Weibchen erhielten eher den ersten Futteranteil, aber erhielten nicht mehr Futter insgesamt, was wahrscheinlich durch eine grössenabhängige Dominanz der Männchen über nicht-monopolizierbares Futter erklärt werden kann. Es ist daher unwahrscheinlich, dass die beschriebene erhöhte Sterblichkeit der Männchen auf einen Nachteil der Männchen in der Nestlingskonkurrenz zurückgeführt werden kann. Die erhöhte Sterblichkeit ist eher eine Konsequenz von erhöhtem Futterbedarf und erhöhter Anfälligkeit für schlechte Eiqualität, wie frühere Studien nahelegen.

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