

Parental food conditions affect sex-specific embryo mortality in the yellow-legged gull (*Larus michahellis*)

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Abstract Different mortality of males and females during early post-hatching development in sexually size-dimorphic bird species is usually attributed to different nutritional requirements of the sexes, because mortality is mostly biased toward the larger sex. We investigated whether sex-specific embryo mortality in the yellow-legged gull (*Larus michahellis*), a size-dimorphic seabird, depends on parental condition. To test this, we experimentally modified parental nutritional conditions by supplementary feeding of yellow-legged gulls during egg formation, to evaluate sex-biased environmental sensitivity of gull embryos. We found that eggs were larger in supplemented clutches, but egg size did not affect embryo survival. Survival of male gull embryos was more related to parental food conditions than was survival of female embryos. Survival of male embryos in supplemented clutches was greater than in unsupplemented clutches whereas survival of female embryos was similar in both groups. Because size at hatching was similar in both sexes our results suggest that male phenotype disadvantage is not exclusively linked to the energy demands of size-dimorphic development at the embryo stage.

Keywords Embryo · Nutritional condition · Male disadvantage · Sex-specific survival · Sexual size dimorphism

Introduction

For many bird species male and female mortality is different during early post-hatch development, particularly under poor environmental conditions (Clutton-Brock 1991). In size-dimorphic animals it has been argued that the different sizes of the sexes is one of the main causes of the different mortality (Røskaft and Slagsvold 1985; Nager et al. 2000; Daunt et al. 2001). Thus, it has often been assumed that the larger sex needs more energy during growth to reach its final size and is, therefore, more vulnerable to food shortage (Anderson et al. 1993; Krijgsveld et al. 1998; Velando 2002). Individuals of the larger sex have higher total energy demand (Fiala 1981; Teather 1987; Teather and Weatherhead 1988; Anderson et al. 1993) and presumably require more food to fuel growth than the smaller sex (review in Anderson et al. 1993; but see Newton 1978; Richter 1983; Stamps 1990). In many species in which males are the larger sex, mortality rates are higher for males during post-natal development (Clutton-Brock et al. 1985; Røskaft and Slagsvold 1985; Cooch et al. 1997; Nager et al. 2000) and in birds and mammals this male-biased mortality is correlated with the extent of sexual size dimorphism at maturity, which suggests a causal relationship between size and vulnerability (Clutton-Brock et al. 1985). The role of size dimorphism in sex-biased mortality is emphasized by studies showing that in those bird species in which the females are the larger sex, mortality is female-biased (e.g. Torres and Drummond 1997; Dijkstra et al. 1998; Kalmbach et al. 2005) and that in monomorphic species mortality of the sexes is no different (Sheldon et al. 1998; Szczyz et al. 2005; but see González-Solís et al. 2005).

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It has, however, also been suggested that other mechanisms, unrelated to size, can explain observed sex-specific mortality patterns. The “male phenotype disadvantage hypothesis” posits that some specific male characteristics, for example the high levels of androgens needed for male sexual differentiation, are responsible for the different male vulnerability (Olsen and Kovacs 1996; Müller et al. 2003; Uller and Olsson 2003; Müller et al. 2005). Supporting evidence for this hypothesis is provided by results from a study of kestrels (*Falco tinnunculus*) the females of which are the larger sex. This study showed that male, but not female, nestlings had a reduced immune response under food-stressed conditions (Fargallo et al. 2002). Male-biased mortality has, moreover, been reported under good development circumstances but with low egg quality (Nager et al. 1999). The development of sexual differences begins during embryonic development (Balthazart and Adkins-Regan 2003) when males and females do not differ in their growth, and in some species maternal androgens are higher in male eggs (Bowden et al. 2000; Petrie et al. 2001) and during faster development (Cook and Monaghan 2004). These differences may be important in the male phenotype disadvantage (Müller et al. 2005) and, indeed, the few studies that have studied sex-specific mortality during the embryo phase reported male-biased mortality in monomorphic species (tree swallows, *Tachycineta bicolor*, Whittingham and Dunn 2001; zebra finches, *Taeniopygia guttata*, Rutkowska and Cichon 2002).

In gulls, in which the male is the larger sex, male-biased mortality during the nestling phase has been reported (Sayce and Hunt 1987; Griffiths 1992; Nager et al. 1999, 2000). Male chicks are heavier and more susceptible to starvation (Sayce and Hunt 1987; Griffiths 1992). In lesser black-backed gulls (*Larus fuscus*) male chick survival was severely reduced in broods reared by parents in poor condition, but female chick survival was unaffected by parental condition. Egg size and quality also affect male, but not female, post-hatching mortality (Nager et al. 1999). It has therefore been argued that differences between energy requirements are responsible for male-biased mortality (Nager et al. 2000). If size differences are responsible for male vulnerability, no sex-specific mortality is expected when energy requirements and growth are similar for both sexes. In gulls, male and female embryos do not differ in size at hatching (Griffiths 1992), suggesting similar energy requirements. Thus, if sex-specific mortality depending on environmental/maternal conditions is observed for embryo gulls, this should be attributed to male embryo vulnerability to sex-specific developmental conditions different from size, for

example androgen concentrations (Balthazart and Adkins-Regan 2003; Müller et al. 2005).

In this study we investigated sex-specific embryo mortality in the yellow-legged gull (*Larus michahellis*), a sexually size-dimorphic seabird, in which adult males are 15–20% heavier than females during the breeding season (Alonso-Alvarez and Velando 2003). The resources acquired during the week before laying can be stored by gulls for egg formation and food supplementation during the pre-laying and egg-laying period; this has a large effect on parental condition and, consequently, on egg-size and egg-yolk content (Brown 1967; Parsons 1976; Bolton et al. 1992; Nager et al. 1999; Verboven et al. 2003). We modified embryo conditions experimentally by supplementary feeding of yellow-legged gulls during egg formation to evaluate whether there are sex differences in embryo mortality and whether embryo mortality is affected by nutrient availability in the eggs. If male embryo vulnerability is affected by egg quality, male-biased mortality should be reduced in supplemented clutches.

Methods

The study was conducted on Illas Cíes (Ría de Vigo, Galicia, NW Spain), between April and June 2003. The Islas Cíes have a nesting population of yellow-legged gulls numbering approximately 25,000 breeding pairs (Munilla 1997). The gulls build their nests on high cliffs on the west coast of the islands and lay between one and three eggs, where the latter is modal. In this colony there is low interannual variation in the timing of laying, and the first eggs are laid between the last week of April and the first week of May (unpublished data). In a large breeding area we tagged 80 nest sites on April 26, approximately 2 weeks before the expected laying date. Previous studies of gulls showed that food supplementation had no effect on clutch size and laying date (Bolton et al. 1992). The nest-sites were randomly allocated to either the control or enhanced-body-condition groups. Enhanced-body-condition pairs received ca 200 g sardine (*Sardina pilchardus*) every night for four days and ca 190 g boiled hen's eggs every day during the next 4 days, food was placed very close to the nest and direct observations confirmed that only the supplemented pairs received the food. The control nest-sites were visited in the same way as the supplemented nests but food was not given. During the laying period the eggs were marked and egg length and breadth were measured (to the nearest 0.01 mm) to enable calculation of egg volume (Hoyt 1979). Sample size was reduced because 11 pairs did not lay

(supplemented, 5 pairs; unsupplemented, 6 pairs), 14 clutches were predated (supplemented, 6 clutches; unsupplemented, 8 clutches), and 16 eggs were infertile or contained embryos which died very early (supplemented, 10 eggs; unsupplemented, 6 eggs). Nests were checked daily around the expected day of hatching. On the day of hatching we marked the chicks with a coloured velcro strip according to their hatching order and measured their body mass and tarsus length. We obtained a blood sample (100 µL) from the wing brachial vein for molecular sex determination. The unhatched embryos were collected and preserved in ethanol for DNA extraction.

DNA was extracted from blood with a NaOH extraction method, and from tissue with an LiCl procedure. Sex was determined by PCR amplification of part of two CHD genes present on the sex chromosomes (Griffiths et al. 1998). The fragments of the CHD1 genes located on the Z and W chromosomes were distinguished on the basis of different intron sizes. Females were characterized by two products of different size (ZW) whereas for males only one product (ZZ) was obtained. The primers used were 2550F and 2718R (Fridolfsson and Ellegren 1999).

Nest data were analysed using a general linear modelling technique with Poisson errors and a natural logarithm link for clutch size and with binomial errors and logit link for sex ratio, where the dependent variable was the number of males in the brood and the binomial denominator was the number of fertile eggs. To account for clustering as a result of nest identity, egg/chick data were analysed using general mixed models (GLMM) with nest identity as the random factor with Satterthwaite correction, for degrees of freedom using the GLIMMIX macro in SAS. We initially included treatment, clutch size, egg position (first, second, third), laying date (in Julian days), egg volume (except in egg-volume analysis), embryo sex, and their interactions as fixed factors. Embryo survival was modelled specifying a binomial error distribution and egg volume; hatchling weight and tarsus length were modelled specifying a normal error distribution and an identity link. All two-way interactions and main factors were included in the initial model and final models were developed using backward elimination. Two-way interactions were removed first, then the main effects. Data are expressed as mean±SE. The level of significance was $P \leq 0.05$

Results

A total of 24 unsupplemented and 30 supplemented nests were studied. Food provision started

10.0±1.1 days before egg laying (range 3–18 days). Clutch size, laying date, and embryo sex ratio did not differ between experimental groups ($P > 0.1$). Egg volume varied substantially with position in the laying sequence ($F_{2,89.2} = 26.68$, $P < 0.0001$) and was 8% greater in the clutches of supplemented parents than in those of unsupplemented gulls ($F_{1,51.8} = 6.18$, $P = 0.016$). Eggs in earlier clutches were, moreover, larger than those laid later ($F_{1,51.4} = 7.06$, $P = 0.010$). Embryo sex, clutch size, and interactions were not related to egg volume ($P > 0.3$). Overall, 79.6% of embryos survived until hatching ($n = 133$ eggs). Embryo survival was strongly affected by laying sequence (Table 1), and 96% ($n = 50$), 90% ($n = 51$), and 74% ($n = 30$) of embryos survived until hatching in the first, second, and third eggs, respectively. Whereas survival was similar for female embryos, survival of male embryos was greater in clutches of supplemented parents than those of unsupplemented parents (Fig. 1, Table 1). Clutch size, laying date, egg volume, and second order interactions did not affect embryo survival and were not included in the final model (P always > 0.05).

Hatchlings from supplemented pairs were 9% heavier than those from unsupplemented pairs ($F_{1,48.7} = 4.55$, $P = 0.038$) although the significant effect disappeared when adjusted for egg volume ($F_{1,51.1} = 0.02$, $P = 0.90$). Thus in the body-mass model only egg volume was significant ($F_{1,84.2} = 149.51$, $P < 0.0001$). Tarsus length at hatching, as a measure of body size, was larger for early embryos hatched in the first positions (laying date, $F_{1,53.7} = 4.75$, $P = 0.034$; laying sequence, $F_{2,92.6} = 5.04$, $P = 0.008$); hatchlings from larger eggs were larger ($F_{1,76.7} = 9.24$, $P = 0.0001$). Body size at hatching was not related to hatchling sex, supplement treatment, or second-order interactions (P always > 0.07).

Table 1 Results from the final general mixed model of embryo survival (modelled specifying a binomial error distribution and logistic link)

Source of variation	Estimate	SE	F	df	P
Laying sequence	-7.23	1.42	30.55	2, 109	<0.001
Treatment	5.17	2.17	0.80	1, 46.1	0.376
Sex	4.35	1.31	0.15	1, 119	0.702
Treatment×sex	-6.92	1.72	16.09	1, 118	0.0001

All two-way interactions and main factors (clutch size, laying sequence, laying date, egg volume, and embryo sex) were included in the initial model, and the final model was developed using backward elimination

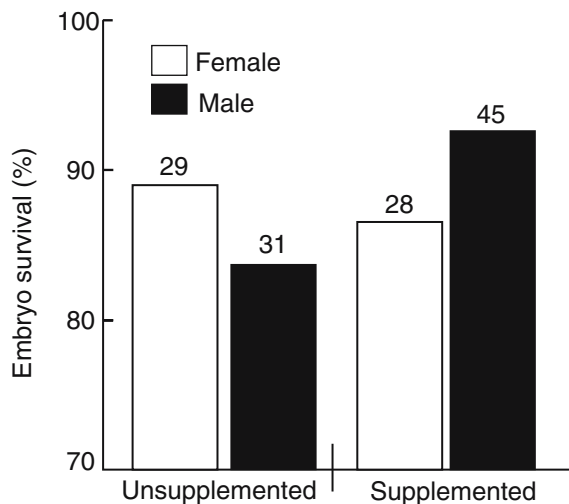


Fig. 1 Survival (proportion) of male (*black*) and female (*white*) embryos of the yellow-legged gull from clutches laid by unsupplemented and supplemented females

Discussion

The results of this study showed that survival of male, but not female, embryos was affected by parental food conditions. Embryo growth was not affected by sex—body mass and size were similar for male and female hatchlings. Male embryos were, therefore, more dependent on parental food conditions than female embryos. The results are consistent with those obtained for lesser black-backed gulls and for black-headed gulls (*Larus ridibundus*), the male chicks of which were more vulnerable than females during post-hatch early development, at an age when males and females did not yet differ in their growth (Griffiths 1992; Müller et al. 2005) or metabolic rates (Eising et al. 2003). Although the larger sex presumably requires more food to fuel growth than the smaller sex (Anderson et al. 1993), these results suggest that other male phenotype traits must also be responsible for male-biased environmental sensitivity in size-dimorphic gulls and agree with studies of early sex-specific mortality in monomorphic species (teasing apart the effect of final size on male phenotype; see Kalmbach et al. 2005).

Different survival of male embryos in the two groups suggests that sex-specific vulnerability depends on egg or incubation quality. We have no data from evaluation of the effect on incubation quality of supplementary feeding during courtship, although a study of lesser black-backed gulls showed that hatchling weight and size was affected by egg size but not by parental quality (measured as the ability to produce large eggs; Bolton 1991). In the current study, eggs

were larger in clutches from supplemented parents, indicating that females in the supplemented group were in better nutritional condition than those in the control group. If the maternal condition of gulls was manipulated by supplementary feeding, extra protein diets increase yolk content of the c-egg (Bolton et al. 1992). Maternal effects that operate via the eggs may be important and, for instance, larger eggs provide greater lipid and water resources (Williams 1994; Kennamer et al. 1997). Nevertheless, in our experiment egg size and the interaction between egg size and sex did not affect embryo survival. The effect of egg size on embryo survival may be obscured by the covariation with laying sequence and supplemental feeding, factors included in the final model. Nevertheless, the effect of egg size on embryo survival remained non-significant ($P=0.49$) when laying sequence and treatment were removed from the model; similarly, egg size did not affect the probability of hatching in black-backed gulls (Bolton 1991). These results suggest that factors other than the egg resources available for embryos were responsible for sex-specific embryo mortality. Female and male embryos reached similar sizes at hatching, although it is possible there were different growth patterns during the embryo stage. Thus, for example, in house finches (*Carpodacus mexicanus*) male oocytes grow more quickly and reach ovulation size earlier than female oocytes during the preovulation stage (Young and Badyaev 2004). It is possible that to achieve larger size later in life, developmental processes early in life must already be different from those in the smaller sex. More studies on sex-specific growth requirements during the embryo stage with varying patterns of size dimorphism are required to clarify these patterns.

In addition to egg size, supplementary feeding may have affected allocation of physiologically active compounds incorporated into eggs, for example carotenoids, antibodies, or hormones (Schwabl et al. 1997; Gil et al. 1999; Saino et al. 2002). In black-backed gulls, females in enhanced condition produced higher-quality eggs with lower concentrations of androgens than those produced by control females (Verboven et al. 2003). High concentrations of androgens in the yolk of eggs in lighter clutches may compensate for poor nutritional quality of eggs (Groothuis and Schwabl 2002), because high concentrations of androgens may benefit chick growth under stressful conditions (Lipar and Ketterson 2000; Eising et al. 2001; Lipar 2001; Godsave et al. 2002). Nevertheless, high levels of androgen (of maternal origin and androgens produced during development) may also be costly for embryo development, because

androgens are immunosuppressors (Grossman 1985; Olsen and Kovacs 1996; Klein 2000) and cause oxidative stress in a wide range of tissues (von Schantz et al. 1999). In birds, the development of sexual differences begins during embryonic development (Balthazart and Adkins-Regan 2003), during which male embryos produce much higher concentrations of androgens (Ottinger et al. 2001), and may be more vulnerable to high concentrations of androgens in the yolk. Differences between amounts of maternally derived yolk testosterone in clutches from supplemented and unsupplemented females, as found in black-backed gulls (Verboven et al. 2003), may explain the male-biased mortality in clutches of unsupplemented parents observed in our experiment. A recent study of black-headed gulls showed that blocking maternal androgens with flutamide had positive consequences (in terms of growth and immunity) for male chicks but negative effects for female chicks (Müller et al. 2005), suggesting that maternal androgens may be related to male phenotypic disadvantage. Future studies should address how prenatal androgen exposure affects sex-specific embryo mortality.

Given the different survival of male embryos and their greater sensitivity to environmental conditions, females may distribute their resources differently according to the sex of the egg. Thus, for example, females invest more resources in eggs of male embryos (Anderson et al. 1997; Cordero et al. 2000; Arnold and Griffiths 2003). That male embryos suffer a fitness disadvantage if their mothers are in poor condition can also be a selective force for sex ratio manipulation (Trivers and Willard 1973; Charnov 1982; Frank 1990). The results of experimental and observational studies of gulls suggest that females adjust the sex of embryos depending on their own condition (Nager et al. 1999; Alonso-Alvarez and Velando 2003). We found the same primary sex-ratio skew; in supplemented clutches it was male biased (0.64) in comparison with unsupplemented clutches (0.49), although differences fell close to significance (logistic regression, $P=0.11$).

In conclusion, we found that male gull embryos were more vulnerable to parental nutritional conditions; current evidence suggests that, because hatchling size was similar for both sexes, male phenotype disadvantage is not exclusively linked to the energy demands of size-dimorphic development. The results suggest that sex-biased mortality during the embryo stage may be important in determining hatchling sex ratios, and should be considered in studies of secondary sex-ratio variation.

Zusammenfassung

Elterliche Ernährungsbedingungen beeinflussen die geschlechtsspezifische Embryonensterblichkeit von Mittelmeermöwen (*Larus michahellis*)

Die unterschiedliche Sterblichkeit von Männchen und Weibchen dimorpher Vogelarten nach dem Schlüpfen wird generell auf geschlechtsspezifische Anforderungen in der Ernährung zurückgeführt, denn die Sterblichkeit des größeren Geschlechts ist meist erhöht. Wir untersuchten, ob geschlechtsspezifische Embryonenmortalität bei der dimorphen Mittelmeermöwe von der elterlichen Kondition abhängt. Um eine geschlechtsabhängige Sensitivität der Embryonen gegenüber Umweltbedingungen zu prüfen, manipulierten wir die elterliche Kondition durch ergänzende Nahrungsgaben während der Eiproduktion. Eier von Paaren mit Zusatzfutter waren größer als die der Kontrollgruppe, aber die Eigröße beeinflusste das Überleben der Embryonen nicht. Die Überlebensrate der männlichen Embryonen war stärker von den elterlichen Ernährungsbedingungen abhängig als die der weiblichen Embryonen: Männliche Embryonen von Eltern, die Zusatznahrung erhielten, hatten höhere Überlebensraten, während weibliche Embryonen keine unterschiedlichen Überlebensraten zwischen den Versuchsgruppen zeigten. Da die Größe der Schlüpflinge beiderlei Geschlechts aber sehr ähnlich ist, deuten die Befunde darauf hin, dass der Überlebensnachteil des männlichen Phänotyps nicht ausschließlich durch größenbedingten Energiebedarf während der Embryonalentwicklung zu erklären ist.

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