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ORIGINAL ARTICLE

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 biassed 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-biassed 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

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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-biassed 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-biassed mortality is emphasized by studies showing that in those bird species in which the females are the larger sex, mortality is female-biassed (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; Szczys et al. 2005; but see González-Solís et al. 2005).

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-biassed 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-biassed 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-biassed 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-biassed 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-biassed 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

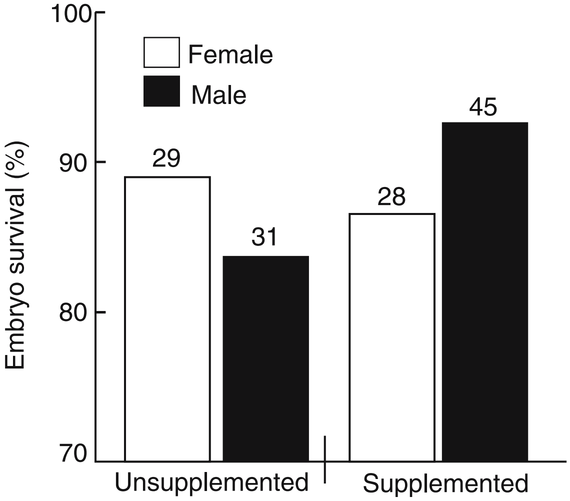

Fig. 1 Survival (proportion) of male (*black*) and female (*white*) embryos of the yellow-legged gull from clutches laid by unsupplemented and supplemented females

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-biassed 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-biassed 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 biassed (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-biassed 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 Phänotpys nicht ausschließlich durch größenbedingten Energiebedarf während der Embryonalentwicklung zu erklären ist.

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References

Alonso-Alvarez C, Velando A (2003) Female body condition and brood sex ratio in yellow-legged gulls *Larus cachinnans*. Ibis 145:220–226

Anderson DJ, Reeve J, Gomez JEM, Weathers WW, Hutson S, Cunningham HV, Bird DM (1993) Sexual size dimorphism and food requirements of nestling birds. Can J Zool 71:2541–2545

Anderson DJ, Reeve J, Bird DM (1997) Sexually dimorphic eggs, nestling growth and sibling competition in American kestrels *Falco sparverius*. Funct Ecol 11:331–335

Arnold KE, Griffiths R (2003) Sex-specific hatching order, growth rates and fledging success in jackdaws *Corvus monedula*. J Avian Biol 34:275–281

Balthazart J, Adkins-Regan EA (2003) Sexual differentiation of brain and behaviour in birds. In: Pfaff D, Arnold A, Etgen A, Fahrbach S, Rabin R (eds) Hormones, brain and behaviour. vol IV. Elsevier, The Netherlands

Bolton M (1991) Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. J Anim Ecol 60:949–960

Bolton M, Houston D, Monaghan P (1992) Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. J Anim Ecol 61:521–532

Bowden RM, Ewert MA, Nelson CE (2000) Environmental sex determination in a reptile varies seasonally and with yolk hormones. Proc R Soc Lond B 267:1745–1749

Brown RGB (1967) Breeding success and population growth in a colony of herring and lesser black-backed gulls Larus argentatus and *L. fuscus*. Ibis 109:502–515

Charnov EL (1982) The theory of sex allocation. (eds) Princenton University Press, Princenton

Clutton-Brock TH (1991) The evolution of parental care. (eds) Princeton University Press, Princeton

Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133

Cooch E, Lank D, Robertson R, Cooke F (1997) Effects of parental age and environmental change on offspring sex ratio in a precocial bird. J Anim Ecol 66:189–202

Cook MI, Monaghan P (2004) Sex differences in embryo development periods and effects on avian hatching patterns. Behav Ecol 15:205–209

Cordero PJ, Griffith SC, Aparicio JM, Parkin DT (2000) Sexual dimorphism in house sparrow eggs. Behav Ecol Sociobiol 48:353–357

Daunt F, Monaghan P, Wanless S, Harris MP, Griffiths R (2001) Sons and daughters: age-specific differences in parental rearing capacities. Funct Ecol 15:211–216

Dijkstra C, Daan S, Pen I (1998) Fledging sex ratios in relation to brood size in size-dimorphic altricial birds. Behav Ecol 9:287–296

Eising CM, Eikenaar C, Schwabl H, Groothuis TGG (2001) Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. Proc Roy Soc Lond B 268:839–846

Eising CM, Visser GH, Müller W, Groothuis TGG (2003) Steroids for free? No metabolic costs of elevated maternal androgen levels in black-headed gull. J Evol Biol 296:3211–3218

Fargallo AJ, Laaksonen T, Pöyri V, Korpimaki E (2002) Intersexual differences in the immune response of Eurasian kestrel nestling under food shortage. Ecol Let 5:95–101

Fiala KL (1981) Reproductive cost and the sex ratio in red-winged blackbirds. In: Alexander RD, Tinkle DW (eds) Natural selection and social behaviour. Chiron Press, New York, pp 198–214

Frank SA (1990) Sex-allocation theory for birds and mammals. Annu Rev Ecol Syst 21:13–55

Fridolfsson A, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Gil D, Graves J, Hazon N, Wells A (1999) Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286:126–128

Godsave SF, Lohmann R, Vloet RPM, Gahr M (2002) Androgen receptors in the embryonic zebra finch hindbrain suggests a function for maternal androgens in the perihatching survival. J Comp Neurol 453:57–70

González-Solis J, Becker PH, Wendeln H, Wink M (2005) Hatching sex ratio and sex specific chick mortality in common terns *Sterna hirundo*. J Ornithol 146:235–243

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

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075

Groothuis TGG, Schwabl H (2002) The influence of laying sequence and habitat characteristics on maternal yolk hormone levels. Funct Ecol 16:281–289

Grossman CJ (1985) Interactions between the gonadal steroids and the immune system. Science 227:257–261

Hoyt DF (1979) Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77

Kalmbach E, Furness RW, Griffiths R (2005) Sex-biassed environmental sensitivity: natural and experimental evidence from a bird species with larger females. Behav Ecol 16:442–449

Kennamer RA, Alsum SK, Colwell SV (1997) Composition of wood duck eggs in relation to egg size, laying sequence and skipped days of laying. Auk 114:479–487

Klein SL (2000) The effects of hormones on sex differences in infection: from genes to behaviour. Neurosci Biobehav Rev 24:627–638

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

Lipar JL (2001) Yolk steroids and the development of the hatching muscle in nestling European starlings. J Avian Biol 32:231–238

Lipar JL, Ketterson ED (2000) Maternally derived yolk testosterone enhances the development of the hatching muscle in the red-winged blackbird *Aegelius phoeniceus*. Proc Roy Soc Lond B 267:2005–2010

Müller W, Groothuis TGG, Dijkstra C (2003) Inter-sexual differences in T-cell-mediated immunity of black-headed gull chicks (*Larus ridibundus*) depend on the hatching order. Behav Ecol Sociobiol 55:80–86

Müller W, Groothuis TGG, Eising CM, Dijkstra C (2005) An experimental study on the causes of sex-biassed mortality in the black-headed gull – the possible role of testosterone. J Anim Ecol 74:735–741

Munilla I (1997) Estudio de la población y ecología trófica de la gaviota patiamarilla. PhD dissertation. University of Santiago de Compostela, Spain

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R (1999) Experimental evidence that offspring sex ratio varies with maternal condition. Proc Natl Acad Sci USA 96:570–573

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

Newton I (1978) Feeding and development of sparrowhawk nestlings. J Zool (Lond) 184:465–487

Olsen NJ, Kovacs WJ (1996) Gonadal steroids and immunity. Endocr Rev 17:369–384

Ottinger MA, Pitts S, Abelnabi MA (2001) Steroid hormones during embryonic development in Japanese quail: plasma, gonadal and adrenal levels. Poultry Sci 80:795–799

Parsons J (1976) Factors determining the number and size of eggs laid by the herring gull. Condor 78:481–492

Petrie M, Schwabl H, Brande-Lavridsen N, Burke T (2001) Sex differences in avian yolk hormone levels. Nature 412:498

Richter W (1983) Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. Am Nat 121:158–171

Røskaft E, Slagsvold T (1985) Differential mortality of male and female offspring in experimentally manipulated broods of the rook. J Anim Ecol 54:261–266

Rutkowska J, Cichon M (2002) Maternal investment during egg laying and offspring sex: an experimental study of zebra finches. Anim Behav 64:817–822

Saino N, Bertacche V, Ferrari RP, Martinelli R, Møller AP, Stradi R (2002) Carotenoid concentration in barn swallow eggs is influenced by laying order, maternal infection and paternal ornamentation. Proc R Soc Lond B 269:1729–1733

Sayce JR, Hunt GL (1987) Sex ratios of prefledging western gulls. Auk 104:33–37

von Schantz T, Bensch S, Grahn M, Hasselquist D, Wittzell H (1999) Good genes, oxidative stress and condition-dependent sexual signals. Proc R Soc Lond B 266:1–12

Schwabl H, Mock DW, Gieg JA (1997) A hormonal mechanism for parental favouritism. Nature 386:231

Sheldon BC, Merilä J, Lindgren G, Ellergren H (1998) Gender and environmental sensitivity in nestling collared flycatchers. Ecology 79:1939–1948

Stamps JA (1990) When should avian parents differentially provisions sons and daughters?. Am Nat 135:671–685

Szczys P, Spendelow JA, Nisbet ICT (2005) Sex ratio and early growth patterns of Roseate Tern chicks during five breeding seasons at Falkner Island, Connecticut, USA. Waterbirds 28:273–279

Teather K (1987) Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. Auk 104:635–639

Teather K, Weatherhead PJ (1988) Sex specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. J Anim Ecol 57:658–668

Torres R, Drummond H, (1997) Female-biassed mortality in nestling of a bird with size dimorphism. J Anim Ecol 66:859–865

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Uller T, Olsson M (2003) Prenatal exposure to testosterone increases ectoparasite susceptibility in the common lizard (*Lacerta vivipara*). Proc Roy Soc Lond B 270:1867–1870

Velando A (2002) Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptative sex ratios in the blue-footed booby. Behav Ecol 13:443–449

Verboven N, Monaghan P, Evans DM, Schwabl H, Evans N, Whitelaw C, Nager RG (2003) Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). Proc R Soc Lond B 270:2223–2232

Williams TD (1994) Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol Rev 68:35–59

Whittingham LA, Dunn PO (2001) Survival of extra-pair and within-pair young in tree swallows. Behav Ecol 12:496–500

Young RL, Badyaev AV (2004) Evolution of sex-biassed maternal effects in birds: I. Sex-specific resource allocation among simultaneously growing oocytes. J Evol Biol 17:1355–1366