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Female body condition and brood sex ratio in Yellow-legged Gulls *Larus cachinnans*

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In the Yellow-legged Gull *Larus cachinnans*, males are the larger sex, and show more reproductive variance than females. We predicted that the proportion of male chicks in a brood should increase with female body condition. We investigated brood sex ratio by using DNA markers taken from samples of hatchlings or dead embryos, and female body condition using plasma cholesterol concentration as a reliable indicator. The brood sex ratio of females in good condition was male biased and the sex ratio of females in poor condition was female biased. This relationship was also significant in those nests where all the eggs laid were sexed. Thus, manipulation of embryo mortality cannot explain the biases reported in this study, suggesting that the sex ratio of the eggs was biased prior to laying. These results confirm that sex-ratio manipulation in gulls operates under natural conditions, and supports earlier experimental findings.

When the cost of rearing sons and daughters varies differentially and the survival and reproductive success of one sex is more dependent than the other on the amount of parental resources, breeding females tend to produce more chicks of this sex if those females are in good condition (Trivers & Willard 1973, Charnov 1982, Clutton-Brock 1991). In size-dimorphic birds, the larger sex is more 'expensive' to raise (Fiala & Congdon 1983, Teather & Weatherhead 1988, Wiebe & Bortolotti 1992, Anderson *et al.* 1993, Krijgsveld *et al.* 1998, but see Richter 1983), and can have a higher mortality during the nestling period (Teather & Weatherhead 1989, Griffiths 1992, Torres & Drummond 1997, but see Dhondt 1970). Therefore, in these species, females in poor condition should skew the brood sex ratio in favour of the less expensive sex.

In the last decade sex ratio manipulation has been recorded in several species of birds (e.g. Ellegren *et al.* 1996, Svensson & Nilsson 1996, Komdeur *et al.* 1997). In addition, some studies suggest that the brood sex ratio may be linked to maternal body condition and food availability (Paterson & Emlen 1980, Meathrel & Ryder 1987, Wiebe & Bortolotti 1992, Dzus *et al.* 1996, Komdeur *et al.* 1997, Kilner 1998). Thus, in sexually size-dimorphic species, females produce the less costly sex when food availability is poor (Paterson & Emlen 1980, Wiebe & Bortolotti 1992, Dzus *et al.* 1996, but see Fiala 1981). However, there is little evidence for sex ratio variation with female body condition in dimorphic birds.

One reason for the lack of relevant studies relating the female body condition and sex ratio could be the difficulty of sexing the chicks accurately in the majority of species. However, recent molecular techniques have become available for sexing chicks or even embryos in virtually all avian species, and this has increased the number of studies of avian sex ratios (Griffiths 1992, Graves *et al.* 1993, Lessells *et al.* 1996, Griffiths *et al.* 1998).

A second difficulty when studying sex ratio modification is to find a good index for measuring adult body condition. Recently, plasma metabolites have been proposed as good nutritional indices (e.g. Ferrer 1993, Dabbert *et al.* 1997, Williams *et al.* 1999). The main problem when using these substances is that traits can be specific (see, e.g., Ferrer *et al.* 1987, Jenni-Eiermann & Jenni 1996). A food-deprivation experiment in Yellow-legged Gulls *Larus cachinnans* showed that the best plasma index for individual body condition is cholesterol concentration in plasma (Alonso-Alvarez *et al.* 2002).

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In gulls there is evidence that females can adjust their offspring sex ratio in response to their condition. In Ring-billed Gulls *Larus delawarensis* Ord, chick sex ratio varies in relation to food availability (Meathrel & Ryder 1987). Recently, Nager *et al.* (1999) have shown that Lesser Black-backed Gulls *Larus fuscus* bias the offspring sex ratio when they are under extreme stress (experimental egg removal); those females in poor condition increased the probability of their last eggs being female. In gulls this manipulation seems to be adaptive because maternal condition has a greater effect on the fitness of sons than of daughters. Male chicks are heavier and more susceptible to starvation (Sayce & Hunt 1987, Griffiths 1992). In Lesser Black-backed Gulls male chick survival was strongly reduced in broods reared by parents in poor condition, but female chick survival was unaffected by parental condition (Nager *et al.* 2000). Overall, these studies suggest that female gulls can adjust the sex ratio of their broods in accordance with the potential fitness gain for each sex in relation to their own body condition (Trivers & Willard 1973, Charnov 1982, Frank 1990). Nevertheless, the sex ratio adjustment reported by Nager *et al.* (1999) occurred under extreme experimental conditions. Thus, field studies are now needed to show that sex ratio manipulation also operates in natural populations. In this paper, we examine how the hatching sex ratios of Yellow-legged Gulls vary with female body condition. This species is a monogamous sexually size-dimorphic seabird, in which adult males are 15–20% heavier than females during the breeding season (Cramp & Simmons 1983, present study (mean ± sd): males 966.2 ± 63.1 g, $n = 54$; females 799.6 ± 76.1 g, $n = 46$). We test whether the offspring sex ratio of females in poor body condition is biased towards daughters, which are the smaller sex and more resistant to starvation.

METHODS

The study was carried out on the Islas Cíes (Ría de Vigo, Galicia, north-west Spain), between April and June 1998. The Islas Cíes have a nesting population of Yellow-legged Gulls numbering around 25 000 breeding pairs, perhaps the largest colony in the world (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 three large subcolonies, we tagged 60 nests during the laying period. The distance to the nearest nest and the clutch size were recorded for each focal nest. In 46 nests the adult females were nest-trapped during the incubation period and several morphometries were obtained. The head length, bill depth and tarsus of these individuals were measured with a caliper (±0.05 mm), whereas the wing length was determined using a stopped steel rule (±1 mm). The gulls were then weighed using a spring balance (Pesola, ±10 g).The birds were sexed by means of a discriminant function:

$$D = 1.430(\text{head length}) + 5.135(\text{bill depth}) + 0.114(\text{body mass}) + 0.262(\text{tarsus}) - 366.988,$$

where values of $D > 0$ identified males (Bosch 1996). The results were tested against previously recorded copulatory behaviour (100% of coincidence). A blood sample (2 mL) was collected from the wing brachial vein and anticoagulated with lithium-heparin. Samples were spun in a clinical centrifuge (550 g) and the plasma stored at –20 °C.

In the Yellow-legged Gull, the plasma concentration of cholesterol is a reliable index of body condition (Alonso-Alvarez *et al.* 2002). Through a food-controlled experiment, we found that cholesterol values correlated negatively with the proportion of body mass loss, which included the individual range of body mass, from the individual optimum to a critical level. This individual optimum was reached during two weeks by means of an *ad libitum* diet comprising Sardines *Sardina pilchardus*. Thus, plasma cholesterol explained 75% of the deviance in body mass change (Alonso-Alvarez *et al.* 2002). Figure 1 shows this relationship between the proportion of body mass lost and cholesterol concentration in adult female Yellow-legged Gulls during the cited experiment. Thus, gulls with low plasma cholesterol concentration are in poor body condition, whereas those with high levels of this lipid are in good body condition. The cholesterol plasma concentrations were measured using a spectrophotometer (Hitachi-U2000, Tokyo, Japan) and by applying the cholesterol esterase method (Allain *et al.* 1974, mean of plasma cholesterol = 267.56 mg/dL ± 72.42 sd).

On the first day of hatching, we collected blood samples from the newly hatched chicks of each tagged nest. The blood sample was obtained from each chick by puncturing the wing vein and transferring the blood by using a capillary tube. The unhatched embryos were collected for DNA extraction and preserved in ethanol. Samples were then transported back to the lab in a cool box and stored at –20 °C until DNA extraction. Sex was determined through

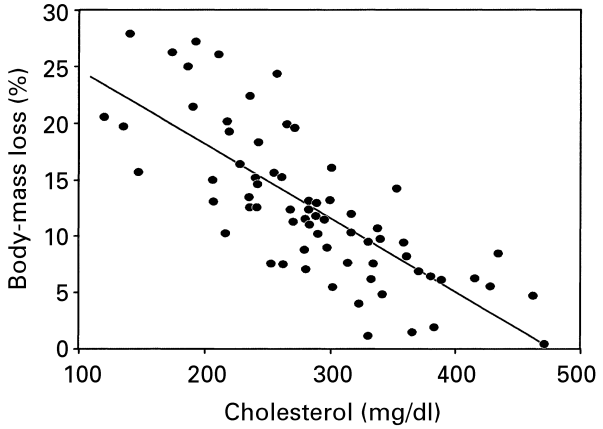

Figure 1. Relationship between cholesterol plasma concentration and the proportion of body mass loss of adult female Yellow-legged Gulls during a food-controlled experiment ($n = 10$). In order to avoid pseudoreplication, the term 'Bird Identity' was included in the model and the calculations were performed on the within-bird variation. The relationship between cholesterol and female body mass loss was significant ($r = 0.81$, $P < 0.001$).

the PCR amplification of CHD gene fragments with primers P2 (5′-TCTGCATCGCTAAATCCTTT-3′), and P8 (5′-CTCCCAAGGATGATRAAYTG-3′) following Griffiths *et al.* (1998). According to this approach, fragments of CHD1 genes located on Z and W chromosomes are both amplified and subsequently distinguished by a difference in their intron size. A single product is obtained from the amplification of a male individual (ZZ), whereas a female (ZW) yields two products of different size that can be distinguished using electrophoresis.

Crude DNA preparations were made by boiling 5 μL of blood in 100 μL of 100 mM NaOH for 10 min; 0.5 μL of the DNA extracts were used as template in a PCR reaction consisting of 67 mM Tris-HCl pH 8.8, 16 mM $(NH4)_2SO_4$, 3.5 mM $MgCl_2$, 0.01% Tween-20, 0.01% gelatine, 200 μM of each dNTP, 0.2 μM of each primer, and 0.5 U of Taq DNA polymerase in a total volume of 25 μL. The PCR reaction was performed in a PTC-100 thermal cycler (MJ Research, Waltham, MA, USA), using an initial cycle of 2 min at 94 °C, 30 s at 55 °C and 1 min at 72 °C, followed by 34 cycles of 30 s at 92 °C, 30 s at 50 °C and 45 s at 72 °C. The reaction was completed with a final run at 72 °C for 5 min. Seven microlitres of the resultant product from the PCR reaction was analysed by electrophoresis in 3.5% agarose gel containing 0.5 μg/mL ethidium bromide. PCR products were then visualized and photographed under UV light. A CHD1-Z band of approximately 340 bp appeared in both sexes, whilst females had a second CHD1-W band of 370 bp. Sex identification was confirmed by using control individuals of known sex ($n = 19$).

Female body mass and cholesterol plasma concentration were not correlated with the laying date, but they were positively correlated with the number of days from laying date to capture date. In order to control this effect on body mass and cholesterol values, we used the residuals from regression of these variables on the number of days from laying date to capture date. In addition, in order to control for the effect of individual differences in body size on body mass, we also used the residuals from regression of wing length on body mass. In order to avoid pseudoreplication, we considered the nest as the unit for statistical analysis. The proportion of males in the brood was analysed by logistic regression analysis with binomial errors and logit links. The dependent variable in the analysis was the number of sons (males) in the brood and the binomial denominator was the brood size (number of nestlings sexed). The degree of discrepancy between the model and the data is given by deviance, which is asymptotically distributed as chi-square (Crawley 1993). The deviation from the binomial model was tested using the deviance of the null model. The chicks in 60 nests were sexed, with a complete sexing of the whole clutch in 33 nests (complete), and the remaining 27 with only a proportion of the offspring sexed (incomplete). The statistical analyses were performed both on all the nests and on just those nests without embryo mortality. Correlation coefficients were calculated by $r = SSXY/(\sqrt{SSX \cdot SST})$, where SSXY stands for the sum of the products x times y, SSX is the sum of squares for x, and SST is the total sum of the squares (Crawley 1993).

RESULTS

One hundred and thirty-one individuals were sexed out of 140 hatchlings (94%) sampled in 60 nests. In addition, six dead embryos were also sexed. Overall, we sexed 78% of the eggs laid ($n = 176$). The sex ratio at hatching did not differ from a 1:1 ratio, with 70 males and 67 females across all nests, and 39 males and 40 females across the complete broods. There was no significant difference between the sex ratio calculated from all data and that from the only complete broods (Mann–Whitney test, $Z = 0.39$, $n = 60$, $P > 0.1$). Sex ratio was unrelated to the proportion of eggs in the clutch for which sex was determined

Table 1. Results from individual logistic regressions of the proportion of hatchling males in a brood. Two separate analyses were performed, one including all nests and one including just nests without embryo mortality (complete broods). Female mass was corrected by calculating the residuals of the linear regression between body mass and wing length (body size). Moreover, female mass and cholesterol plasma levels were corrected by calculating the residuals of the linear regression between these two variables and the number of days from laying date to capture date.

	All nests				Complete broods			
	n	*df*	Change in deviance	Residual deviance	*n*	*df*	Change in deviance	Residual deviance
Laying date	60	1	0.417	37.07	33	1	0.173	10.97
Proportion sexed	60	1	0.088	37.44				
Colony	60	2	1.498	35.98	33	2	0.253	10.89
Nearest nest distance	59	1	0.951	37.36	33	1	0.038	10.99
Clutch size	60	1	0.803	36.68	33	1	0.003	11.14
Brood size	60	1	1.580	35.91	33	1	0.350	10.79
Wing length of female	46	1	0.925	28.49	26	1	0.042	9.04
Female mass	45	1	0.004	28.37	26	1	0.129	8.83
F. mass corrected by laying date	45	1	0.001	28.37	26	1	0.117	8.84
F. mass corrected by wing length	45	1	0.016	28.36	26	1	0.241	8.72
Female cholesterol	46	1	2.919*	26.80	26	1	2.517**	6.56
F. cholesterol corrected	46	1	3.215**	26.50	26	1	2.771**	6.31

*$P < 0.05$; **$P < 0.01$.

(Table 1). The proportion of male hatchlings did not vary either between the subcolonies or with the density (measured as distance to the nearest nest) for either the whole data set or just the complete broods (Table 1).

The adult females were captured at 46 nests, but complete clutches were sexed in only 33 nests. Of the unsexed eggs, 54% ($n = 13$) were infertile. There was a significant positive correlation between the proportion of sons in the brood and the cholesterol plasma level, both in all nests (Table 1, $r = 0.31$, $P = 0.017$) and in the complete broods (Table 1, $r = 0.53$, $P = 0.002$). Moreover, when the cholesterol data were corrected by capture date the correlation with brood sex ratio was also significant, both across all nests (Table 1, $r = 0.33$, $P = 0.012$), and across just the complete broods (Table 1, $r = 0.55$, $P = 0.001$). Therefore, the proportion of males in a brood increased with improving female body condition (Fig. 2). The proportion of sons was unrelated to the clutch size, laying date, the brood size at hatching, the female wing length, the female mass, or the female mass corrected by seasonality or wing length (Table 1). Moreover, the cholesterol concentration in the female plasma was not correlated with either the laying date ($r = –0.19$, $P > 0.1$), density ($r = 0.24$, $P > 0.1$), hatching success ($r = 0.16$, $P > 0.1$) or the female wing length ($r = –0.15$, $P > 0.1$), but female mass was correlated with female plasma cholesterol ($r = 0.29$, $P = 0.05$).

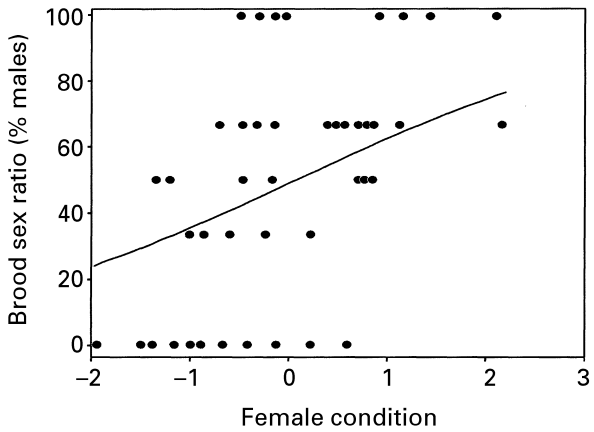

Figure 2. Proportion of sons in relation to female body condition in Yellow-legged Gulls in the Islas Cíes (all broods, $n = 46$). Female body condition was estimated by calculating the residuals of the linear regression between cholesterol concentrations in plasma and the number of days from laying date to capture date. Residuals obtained were standardized in a *Z*-normal distribution. High values of body condition indicate females in good condition and low values indicate females in poor condition. Analyses were performed using logistic regression. Adjusted curve is shown [Proportion of sons = exp (0.55 female body condition – 0.04)/ 1 + exp (0.55 female body condition – 0.04)].

DISCUSSION

In this study, we have found a strong relationship between female body condition and the brood sex ratio. The observed sex ratio differences in relation to

the female condition could have been caused by sex-specific embryo mortality. However, hatching success was unrelated to female body condition, and the brood sex ratio was not correlated with the proportion of eggs sexed in the clutch (Table 1). Moreover, the association between sex ratio and female body condition was also present when we considered only the complete broods. In the nests where the adult female was captured, only six fertile eggs (5% of the total fertile eggs) were not sexed. Female body condition explained 11–30% of the deviance of the observed sex ratio, so the magnitude of embryo mortality alone cannot explain the biases reported in this study. Fiala (1980) suggested that primary sex ratio should always be sampled before the ages at which differential mortality may occur. Sexing several unhatched embryos would have minimized previous sex ratio bias. This investigation therefore represents an example of primary sex ratio modification in birds dependent on maternal condition (Wiebe & Bortolotti 1992, Kilner 1998, Nager *et al.* 1999). Moreover, we have shown a sex-ratio bias that is related directly to female body condition as analysed by a novel and specific index, which was validated to the species studied.

Trivers and Willard (1973) predicted that local deviations from the population sex ratio should occur in direct relation to the resources available to the parents. Several authors have indeed related sex-ratio modifications to food conditions (Paterson & Emlen 1980, Wiebe & Bortolotti 1992, Dzus *et al.* 1996, Kilner 1998, Torres & Drummond 1999). In Ring-billed Gulls, Meathrel and Ryder (1987) reported some evidence of interyear variation in chick sex ratio in relation to food availability. However, in this study we reported sex-ratio modifications linked to individual differences in female body condition under similar levels of food availability. Gulls have recently been shown to bias the offspring sex ratio when they are under extreme stress (experimental egg removal); females in poor condition skewed the sex ratio of their last eggs towards being female (Nager *et al.* 1999). Our study shows that this process occurs naturally in gulls, and confirms that sex-ratio manipulation operates in natural populations.

The variation in sex ratio with maternal fitness could reflect a decline in food availability throughout the breeding season (Howe 1977, Dijkstra *et al.* 1990, Daan *et al.* 1996; Lessells *et al.* 1996, Velando *et al.* 2002, but see Sayce & Hunt 1987, Wiebe & Bortolotti 1992). Although this effect is usually linked to female body condition (Howe 1977, Dijkstra *et al.* 1990, but see Daan *et al.* 1996, Lessells *et al.* 1996), we detected no correlation between laying date and sex ratio. This conclusion is supported by the observation that laying date was not related to female body condition in terms of plasma concentrations of cholesterol, and suggests that body condition does not decline with season. We found no effect of season on hatching success (C. Alonso-Alvarez & A. Velando unpubl. obs.). In another study on gulls (Sayce & Hunt 1987), sex ratio also did not change with laying date. Moreover, it has been reported that fledging success is not correlated with laying date in the closely related Herring Gull *Larus argentatus* (Harris 1969, but see Davis 1975). The Yellow-legged Gull is an opportunistic omnivore with a diverse diet (Munilla 1997), including food supplies of human origin. It is likely that the food availability throughout the breeding season in the Islas Cíes is fairly constant (Munilla 1997).

Sex ratio was correlated with female cholesterol concentration in the plasma, but not to female mass or mass corrected by body size. However, female mass was related to female cholesterol concentration. Mass and cholesterol in plasma may be related to adult body condition. Nevertheless, cholesterol was the best predictor of individual mass optimum in Yellow-legged Gulls (see Alonso-Alvarez *et al.* 2002). There are several reasons why mass may be a poor indicator of body condition: (1) body mass alone, or body mass corrected by body size, does not consider the effect of variability in the individual range of body mass; (2) the use of residuals from regressions of body mass on body size creates misleading results when the body mass does not vary isometrically with body size (see Blem 1984, Piersma & Davidson 1991, Green 2001); and (3) the females were captured during the incubation period and their mass drops in relation to the time since they last left the eggs to feed (Wendeln & Becker 1996).

Additionally, plasma chemicals used as body condition indices can offer information about the physiological health of the birds (see Ferrer 1993, Brown 1996). A decrease in plasma cholesterol levels could be the result of a low rate of anabolic processes. This lipid is involved in forming cell membranes, steroids and bile acids (reviewed by Griminger 1986). Therefore, our results from the food-deprivation experiment in captive Yellow-legged Gulls indicate that cholesterol concentration in plasma is a reliable body condition index for this species (see Fig. 1).

We found that adult female Yellow-legged Gulls in poor condition bias their brood sex ratio towards being female. This bias could be adaptive if female

chicks of this species are less energetically 'expensive' to rear or show lower variance in reproductive success than males (Trivers & Willard 1973, Charnov 1982, Clutton-Brock 1991). As in other dimorphic bird species, the heavier sex (male in the Yellow-legged Gull) should be more expensive to rear (reviews in Anderson *et al.* 1993 and Krijgsveld *et al.* 1998). Male gull chicks are larger, grow faster and have a higher mortality rate than female chicks, probably as a result of their greater susceptibility to starvation (Sayce & Hunt 1987, Griffiths 1992). The survival to fledging of male chicks (but not female chicks) is reduced if they came from females in poor condition (Nager *et al.* 1999, 2000). Moreover, extra investment in males by parents in good body condition might increase the reproductive success of this sex owing to the severe competition that occurs between male gulls for breeding territories (Tinbergen 1956, Coulson 1968, Southern 1981).

In conclusion, females in poor condition could improve their reproductive success by producing more daughters, whereas females in good condition should produce more sons. This study confirms that sex-ratio manipulation in gulls operates in natural populations, and supports earlier studies conducted under extreme experimental conditions.

In the future, other important issues such as the energetic cost to the female of producing and rearing male or female chicks, the consequences of maternal body condition on future breeding success of each sex, and the parental investment devoted to male or female chicks during their growth should be analysed in gulls. Moreover, nothing is known about the physiological mechanism of avian sex allocation. In birds, females are the heterogametic sex, and although the final phase of an oocyte starts about one week before laying, its sex is determined just a few hours before ovulation (e.g. Sheldon 1998). Two potential mechanisms have been proposed to explain sex-ratio manipulation before laying: meiotic drive and atresia (Krackow 1995, Emlen 1997, Sheldon 1998). Meiotic drive would be present if the mother selects the sex of an oocyte. This has not been demonstrated in birds but is known to occur in insects. Meanwhile, atresia occurs when the mother identifies the sex of the secondary oocyte, aborting those of the 'wrong' sex during the few hours before ovulation. Therefore, atresia should be restricted to controlling the sex of the first or the last egg of the laying sequence. Resolving which of these mechanisms the mother gull uses in her sex-ratio manipulation remains a challenge for future research.

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