ORIGINAL ARTICLE

Offspring sex ratio in relation to parental structural size and body condition in the long-lived wandering albatross (*Diomedea exulans*)

Pierrick Blanchard · Nicolas Hanuise · Stéphanie Dano · Henri Weimerskirch

Abstract Sex ratio theory is one of the most controversial topics in evolutionary ecology. Many deviations from an equal production of males and females are reported in the literature, but few patterns appear to hold across species or populations. There is clearly a need to identify fitness effects of sex ratio variation. We studied this aspect in a population of a long-lived seabird, the wandering albatross (*Diomedea exulans*), using molecular sex-identification techniques. We report that parental traits affect both (1) fledgling traits in a sex-dependent way and (2) chick sex: Sons are overproduced when likely to be large at fledging and, to a lesser extent, daughters are overproduced when likely to be in good body condition at fledging. Because for the same population, a previous study reported that post-fledging survival was positively affected by size in males and by body condition in females, our results suggest that wandering albatrosses manipulate offspring sex to increase post-fledging survival.

Communicated by I. Hartley

P. Blanchard (✉)
Laboratoire de Biométrie et Biologie Évolutive,
Université Lyon 1,
69622 Villeurbanne Cedex, France
e-mail: pierrick@biomserv.univ-lyon1.Fr

N. Hanuise
Laboratoire de Physiologie Intégrative,
Cellulaire et Moléculaire, Université Lyon 1,
69622 Villeurbanne Cedex, France

P. Blanchard · S. Dano · H. Weimerskirch
Centre d'Études Biologiques de Chizé,
79360 Villiers en Bois, France

Introduction

Sex allocation theory predicts that parents should adjust their level of investment in sons and daughters in relation to the specific fitness benefits of each sex (Frank 1990). In the late 1980s, sex ratio manipulations in birds were not believed to occur (Clutton-Brock 1986; Weatherhead and Teather 1991), although such biases were theoretically expected (Frank 1990) and a growing body of empirical evidence suggested that they occurred in other groups (Clutton-Brock et al. 1986; Van Shaik and Hrdy 1991). Because sexual dimorphism is often reduced, if not absent, in juvenile birds, only the recent availability of molecular sex identification techniques (Griffiths et al. 1998) has allowed researchers to obtain reliable data on primary sex ratios of birds and to reach a similar conclusion to the other groups: an unconvincing general pattern (Hasselquist and Kempenaers 2002; West et al. 2002; Pike and Petrie 2003). Among vertebrates, sex ratio theory has been deeply investigated mainly in two groups: birds (Pike and Petrie 2003) and ungulates (Hewison and Gaillard 1999; Sheldon and West 2004). Inconsistent results within and across species have been reported both for birds (within, Radford and Blakey 2000; across, Pike and Petrie 2003) and ungulates (within, Kruuk et al. 1999a; across, Hewison and Gaillard 1999; Sheldon and West 2004). In both groups, some studies failed to detect any skew in sex ratio even when expected (birds, Westerdahl et al. 1997; ungulates, Blanchard et al. 2005), whereas others reported bias with no apparent adaptive explanation (birds, Heinsohn et al. 1997; ungulates, Wauters et al. 1995).

Studies reporting sex ratio skews in birds usually propose a meaningful verbal adaptive explanation (Hasselquist and Kempenaers 2002). However, only a few studies are based on correlations (Dijkstra et al. 1990; Daan et al.

1996; Appleby et al. 1997; Fletcher and Hamer 2004) or experimental approaches (Komdeur et al. 1997; Komdeur 1998; Nager et al. 1999, 2000; Badyaev et al. 2002) which gave compelling evidence for fitness effects of sex ratio variation in birds. Clearly, there is a need to identify effects of sex ratio variation on reproduction or survival. One of the reasons for such a shortage probably deals with the rarity of long-term monitoring data, especially for long-lived species, such as Procellariiformes (petrels and albatrosses). The largest Procellariiforme, the wandering albatross (*Diomedea exulans*), has the longest chick-rearing period among birds, produces a fledgling only every 3–4 years, and adult survival is extremely high (Weimerskirch et al. 1997a). Like all Procellariiforms, they also lay a single egg. This makes the study of sex ratio manipulation easier, as the effect of number, quality and sex of the offspring are not confounded (Williams 1979). This may also increase the probability of a facultative adjustment in sex ratio to occur (Sheldon 1998).

Weimerskirch et al. (2000) reported that factors affecting post-fledging survival strongly differed according to sex in this long-lived species. The probability of survival from fledging to adulthood was positively related to fledging structural size for male chicks and to fledging body condition for females. Chick provisioning (Weimerskirch and Lys 2000), foraging patterns and habitat selection (Shaffer et al. 2001) are well documented in this species. They suggest that parental traits (i.e. structural size and body condition) may affect fledgling traits in a sex-dependent way. If so, parents could increase their fitness return by producing the sex with the highest probability of survival given its future fledging traits, i.e. according to their traits at egg formation (Trivers and Willard 1973; Frank 1990). Thus, our first goal was to investigate the relationships between the traits of parents and fledglings. We then tested whether parents biased chick sex according to their own traits in a way that favors offspring post-fledging survival.

Materials and methods

The study was carried out on Possession Island, Crozet Archipelago (46°25′S, 51°50′E), from December 2002 to December 2003, on a population monitored since the early 1960s (Weimerskirch et al. 1997a). Birds were chosen randomly at the colonies of Baie du Marin and Pointe Basse.

Parental traits

The measure of body condition in sex ratio studies should be assessed as close as possible to egg formation (Pike and Petrie 2003; Sheldon and West 2004). However, manipulating females may be risky if they carry an egg. Therefore, we measured parents randomly during incubation. To make sure the mass measured during incubation was a relevant index of the mass around egg formation, however, we weighed 12 males and 13 females both before laying and during incubation. In the other parts of the analyses, we considered the mass measured during incubation for homogeneity with the other birds.

Previous studies on the same population reported that body condition and structural size might be relevant parameters to assess parental quality (Weimerskirch et al. 2000; Shaffer et al. 2001). The lengths of tarsus, culmen, head (from the occipital bone to the extremity of the beak), as well as maximum and minimum bill height were measured with vernier calipers, and the wing length with a ruler. To measure structural size, we conducted a principal components analysis using a covariance matrix on these six measurements. As male and female wandering albatrosses greatly differ in size and allometry (Shaffer et al. 2001), they were analysed separately. The coordinates on the first principal component were used as an index of structural size. The proportions of variance explained by the first components were 43 and 36% for females and males, respectively. The body condition was defined as the residuals obtained when body mass was regressed against the index of structural size. Sex and age of the parents were known from a long-term database, banding of chicks before fledging being carried out since 1965 and banding of breeding birds of unknown age since 1959 (Weimerskirch et al. 1997a). For the latter, we assessed a "minimum age" calculated from the year of first recorded breeding adding 7 years, the minimum age at first breeding (Weimerskirch et al. 1997a). We discarded "minimum ages" found to be "smaller than 30" ($n=6$ males and 7 females), as they were not informative (animals could be 29 or 7 years old). We pooled the birds aged 30 years or older.

Chicks molecular sexing

All nests were checked regularly. A total of 17 pairs failed at the egg stage (the sex of the chick was unknown), six around hatching (sex unknown) and six during brooding (four of them were sexed before they died). The other pairs produced 86 fledglings that were sexed before 6 weeks of age. Blood samples (200–300 μl) were collected from the brachial vein of these 90 brooded chicks. The sex was determined by polymerase chain reaction (PCR) amplification of partial fragments of two chromo-helicase-DNA-binding (CHD) genes present on the sex chromosomes (Fridolfsson and Ellegren 1999). DNA was prepared from blood samples using a NaOH extraction method (Wang et al. 1993). Blood cells were disrupted after boiling in 1:30

(v/v) 0.3 M NaOH for 2 min at 100°C to release DNA and was neutralized with 1:10 (v/v) Tris–HCl 0.1 M (pH 8). Amplification was performed in 20-μl final volumes on an Eppendorf thermal cycler using 0.5 U *Taq* DNA polymerase, 200 μM deoxyribonucleotide triphosphate, 10 mM Tris–HCl pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$ and 0.4 μM of primers 2,550F (5′-GTTACTGATTCGTCTACGAGA-3′) and 2,718R (5′-ATTGAAATGATCCAGTGCTTG-3′). The amplification profile consisted of an initial denaturing step of 94°C for 2 min followed by a "touch down" scheme (Don et al. 1991) where the annealing temperature was lowered 1°C per cycle starting from 50°C until a temperature of 42°C was reached. Then, 30 additional cycles were run at a constant annealing of 42°C. Denaturation was at 94°C for 30 s, annealing for 30 s and extension at 72°C for 60 s. A final extension step of 5 min was added after the last cycle. PCR products were separated by electrophoreses for 60 min at 100 V in a 1.8% agarose gel stained with ethidium bromide. Birds were sexed according to the presence of the PCR products of CHD-Z (650 bp, both sexes) and CHD-W (450 bp, females only).

Fledglings traits

To investigate the influence of parental traits on fledgling traits (reported to affect post-fledging survival), a subsample of 67 chicks (31 males and 36 females) was chosen randomly among the sexed chicks and processed every 25–30 days from early November to fledging. We used the measurements taken closest to fledging (i.e. the last records). Structural size and body condition index were assessed as for the adults, to allow reliable comparisons. The proportions of variance explained by the first components were 45.5 and 45.3% for females and males chicks, respectively.

Statistical analyses

Before investigating the effect of parental traits on chick sex and fledgling traits, we tested whether the sex ratio among the 90 sexed chicks was biased or not using a chi-square goodness of fit. We then studied the relationships between the mass of the parents before and after egg formation using linear regressions. We also used linear regressions to check for any assortative mating according to size or condition and to investigate the relationships between parental and fledgling traits.

Then, we investigated the relationships between parental traits and chick sex. In this species, ages of the males and the females in pairs are highly correlated (Jouventin et al. 1999). We therefore considered the age of the pair calculated as the average age of the parents. We also added its square because a previous study reported a quadratic

effect of parental age on chick sex (Weimerskirch et al. 2005). Because the size of the male was correlated with the pair's age, we considered the pair's age and the parental size/condition in two separate analyses.

We performed a logistic multiple regression including structural size and body condition of both parents, with the sex of the chick as the response variable. We tested each effect by successively withdrawing each of the four terms and calculating the difference in deviance, distributed as a *F*. As both parents could not be measured for all chicks, we then performed the same analysis focusing either on the male or the female parent, thereby increasing the sample size by 12 (19%) in both cases. We present both analyses. All statistical analyses used R software (R Development Core Team 2003).

Results

The sex ratio among the 90 chicks sexed soon after hatching was not significantly biased (52 females and 38 males, $\chi^2 = 2.18$, $df = 1$, $p = 0.14$).

The masses of the parents before and after laying were significantly correlated for both females ($F_{1,11} = 5.25$, $p = 0.043$, $R^2 = 0.32$) and males ($F_{1,10} = 12.82$, $p = 0.005$, $R^2 = 0.56$). There was no assortative mating according to size or condition (all $p > 0.08$).

Parents-fledglings correlations

Male chicks were larger at fledging when their mother was large (male fledgling structural size $= 0.62 \times$ maternal structural size -0.54; $R^2 = 0.4$, $F_{1,22} = 14.4$, $p = 0.001$; Fig. 1). Paternal body condition or structural size, or maternal body condition did not influence male fledgling structural size (all three $p > 0.62$). Parental traits did not affect male fledgling body condition (all $p > 0.51$).

Female chick's fledging structural size was also related to mother's structural size (female fledgling structural size $= 0.59 \times$ maternal structural size $+0.06$; $R^2 = 0.325$, $F_{1,32} = 15.4$, $p < 0.001$). The other parental traits did not influence daughter's structural size (all $p > 0.19$). Female fledglings were, though not significantly, in a better condition when their father was in good condition ($F_{1,31} = 4$, $p = 0.054$).

Parents–fledglings correlations are summarized in Table 1.

Pair's age had no influence on male (all $p > 0.39$) or female (all $p > 0.10$) fledglings structural size or condition.

Parental traits and chick sex

Fathers in good body condition produced fewer sons (and thus, more daughters) compared to fathers in poorer body

Fig. 1 Male fledgling structural size in relation to maternal structural size. The coordinates on the first principal component calculated on culmen, maximum and minimum bill height, head, tarsus and wing length, were used as an index of structural size
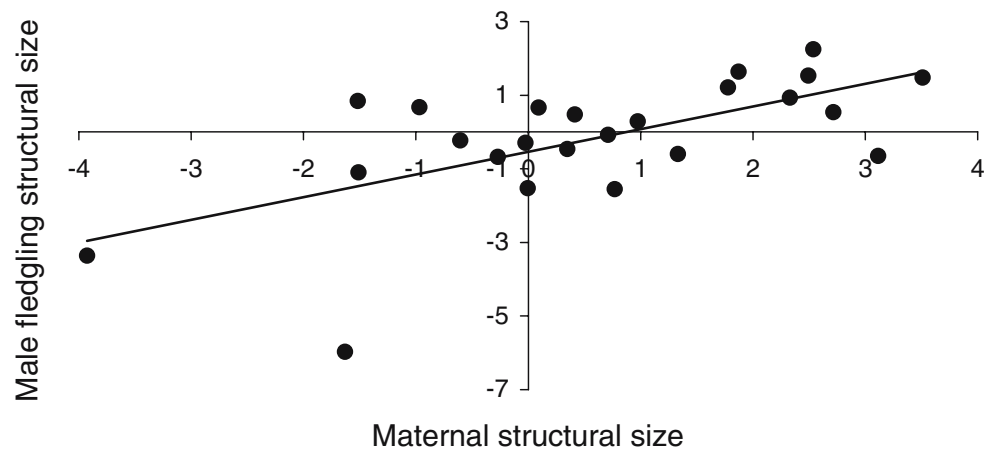
condition (*logit* (male chick)=−0.52 (±SE 0.24)×paternal body condition−0.31(±SE 0.24), $F_{72,73}$=4.8, p=0.03; Table 2). The probability of producing a son was higher for large females (*logit* (male chick)=0.43(±SE 0.18)×maternal structural size−0.54 (±SE 0.25), $F_{72,73}$=6.6, p=0.03; Table 2; Fig. 2). Paternal structural size and maternal condition had no influence on chick sex (both p>0.70). Pair's age did not affect chick sex (p>0.30).

Discussion

A previous long-term study based on the same population reported that post-fledging survival was positively related to fledging size for male and to fledging condition for females (Weimerskirch et al. 2000). In this paper, we report that larger mothers produced more sons compared to the other females, and that their son was also larger at fledging. Thus, our results suggest that sons are overproduced when they are likely to be large at fledging, which will increase their survival probability to adulthood. Our results also suggest that daughters are overproduced when they are likely to be in better condition at fledging, but to a lesser extent given the weaker relationship between paternal and daughter's body condition compared to the relationship

between maternal and son's structural size. Therefore, our results indicate that in wandering albatrosses, the fitness return for parents will be maximized by the production of the sex which will benefit the most from parental characteristics at the time of egg formation in terms of the probability of post-fledging survival.

Sex ratio manipulation may affect parents' fitness through a variety of factors and at different time scales. In Seychelles warblers (*Acrocephalus sechellensis*), daughters often remain on their natal territories as helpers. Whereas this is beneficial to the parents when habitat quality is high, this leads to an increase in competition in poor years (Komdeur et al. 1997). It has been shown that by adjusting offspring sex ratio to food supply, females increased fitness both in the short term from the perspective of the breeding pair (Komdeur et al. 1997) and in the long term through offspring reproductive success (Komdeur 1998). Offspring survival (before or after fledging) is one of the ultimate factors reported to explain sex ratio adjustments. Badyaev et al. (2002) showed that house finch (*Carpodacus mexicanus*) breeding females were able to reduce juvenile mortality of sons and daughters up to 20% by joint modification of the sex and the growth of offspring in relation to position within clutches. In the common tern (*Sterna hirundo*), the chick hatched from the last-laid egg

Table 1 Parents–fledglings correlations of body condition and structural size

|			Fledgling			
			Male		Female	
			Size	Condition	Size	Condition
Parent	Male	Size	NS	NS	NS	NS
		Condition	NS	NS	NS	(+)
	Female	Size	+	NS	+	NS
		Condition	NS	NS	NS	NS

+ positive correlation with $p≤0.001$, (+) positive correlation with p=0.054
NS non significant

Table 2 Model selection for the probability of producing a son

Model	Deviance	df	Models compared	Difference in deviance	Difference in df	p value
For chicks with both parents measured						
(1) General model: *logit*(sex) = Mcon + Msiz + Fcon + Fsiz	76.3	58				
(2): (1) − Mcon	79.6	59	(2) and (1)	3.3	1	0.07
(3): (1) − Msiz	78.6	59	(3) and (1)	2.2	1	0.14
(4): (1) − Fcon	76.3	59	(4) and (1)	0.0	1	0.99
(5): (1) − Fsiz	79.6	59	(5) and (1)	3.3	1	0.07
For chicks with at least their father measured						
(1) General model: *logit*(sex) = Mcon + Msiz	97.4	72				
(2): (1) − Mcon	102.2	73	(2) and (1)	4.8	1	0.03
(3): (1) − Msiz	97.5	73	(3) and (1)	0.1	1	0.73
Selected model: *logit*(sex)=−0.31 (±SE 0.24)−0.52 (±SE 0.24)×Mcon						
For chicks with at least their mother measured						
(1) General model: *logit*(sex) = Fcon + Fsiz	93.4	72				
(2): (1) − Fcon	93.4	73	(2) and (1)	0.0	1	0.97
(3): (1) − Fsiz	100	73	(3) and (1)	6.6	1	0.01
Selected model: *logit*(sex)=−0.54 (±SE 0.25)+0.43 (±SE 0.18)×Fsiz						

Mcon male parent body condition; Msiz male parent structural size; Fcon female parent body condition; Fsiz female parent structural size

Fig. 2 The probability for a chick to be male in relation to its mother's structural size. Confidence intervals are given after Yates' corrections
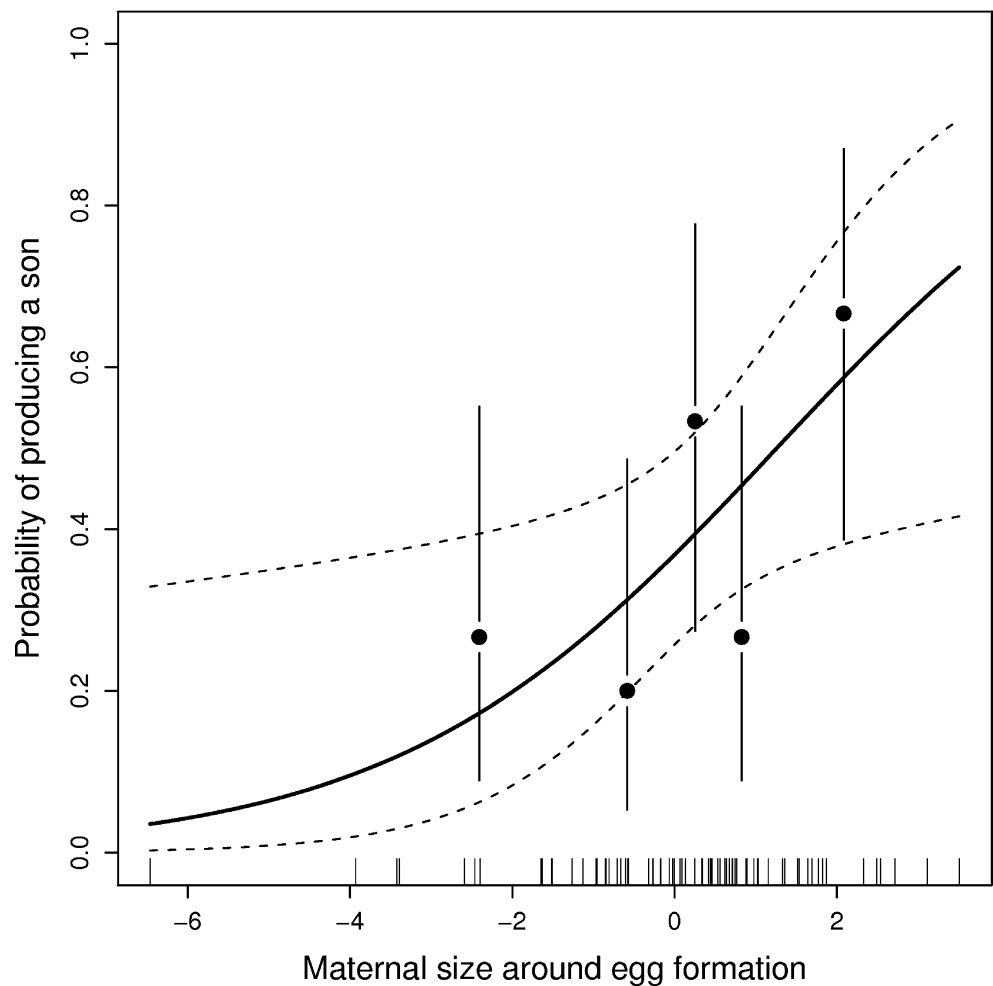
has a low probability of survival to fledging, especially if it is a male (Fletcher and Hamer 2004). Interestingly, females have been reported to bias the sex ratio of this egg towards daughters (Fletcher and Hamer 2004). Hatching timing, but at the scale of the season and not any more within clutches, has also been reported to differently affect sons and daughters' fitness (Hasselquist and Kempenaers 2002). This has been proposed to explain why some sex ratios seasonal variations were probably adaptive (Dijkstra et al. 1990; Pen et al. 1999). In ungulates, most species have polygynous mating systems and exhibit sexual dimorphism. A positive relationship between the phenotypic quality of the mother and the phenotypic quality of the offspring at weaning and during adulthood has been documented in several species (Hewison and Gaillard 1999). Therefore, because male breeding success depends on fighting ability and body size and is more variable than for females, mothers in better than average quality should invest more in sons (Trivers and Willard 1973). Red deer (*Cervus elaphus*) have been reported to meet both the assumptions and the prediction of this model (Kruuk et al. 1999a and references herein).

Beside their importance in such sex allocation theory context, the parents–offspring relationships we report here are also interesting by themselves given the paucity of studies reporting such kind of relationships with known offspring sex. A relationship between parent(s) and offspring body size was reported in tits (e.g. Kölliker et al. 1999) and in another seabird, the snow petrel (*Pagodroma nivea)* although offspring sex was unknown (Barbraud et al. 1999; Barbraud 2000). Parental traits have also been reported to affect offspring condition or body mass (Whittingham and Dunn 2000; Sasvári and Hegyi 2001; Gonzáles-Solis 2004). In our study, whereas maternal size influenced positively fledglings size whatever its sex, paternal condition was positively correlated only to daughter's condition. The former relationship was much stronger probably due to genetic effects (Barbraud 2000), whereas the father-daughter relationship probably involves more "behavioural" effects. Two main chick-provisioning characteristics may help to understand the father–daughter relationship. Firstly, the investment in offspring is under the control of adult condition, i.e. birds invest more when their condition is better (Weimerskirch et al. 1997b). Secondly, whereas mothers deliver more food to sons than to daughters, male parents deliver more food overall than females and provision male and female chicks equally despite the higher requirements of sons given their sexual dimorphism (Weimerskirch and Lys 2000; Shaffer et al. 2001). Other studies revealed a difference in food intake between the sexes that was less than expected based on the dimorphism (e.g. Boulet et al. 2001 and references herein). In ungulates, some studies reported that early traits, such as body mass at birth or at weaning, might affect several life

history traits differently according to offspring sex (Kruuk et al. 1999b; Festa-Bianchet et al. 2000). The relationships between maternal and offspring traits at weaning, or later, have also been investigated, and reports on sex-dependent patterns are common (Hewison and Gaillard 1999).

Because several evolutionary models predict sex ratio biases sometimes in opposite directions and as the underlying physiological mechanisms remain to be identified (Krackow 1995), almost every sex ratio skew can be interpreted as being adaptive (Festa-Bianchet 1996). As underlined by this study, long-term monitoring could be particularly helpful at identifying the potential adaptive value of such patterns and then at distinguishing between sex ratio manipulation, a by-product of sexual selection in the case of dimorphic species, or random variability.

References

Appleby BM, Petty SJ, Blakey JK, Rainey P, MacDonald DW (1997) Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? Proc R Soc Lond B 264:1111–1116

Badyaev AV, Hill GE, Beck ML, Dervan AA, Duckworth RA, McGraw KJ, Nolan PM, Whittingham LA (2002) Sex-biased hatching order and adaptive population divergence in a passerine bird. Science 295:316–318

Barbraud C (2000) Natural selection on body size traits in a long-lived bird, the snow petrel *Pagodroma nivea*. J Evol Biol 13:81–88

Barbraud C, Weimerskirch H, Robertson GG, Jouventin P (1999) Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). J Anim Ecol 68:1179–1192

Blanchard P, Festa-Bianchet M, Gaillard J-M, Jorgenson JT (2005) Maternal condition and offspring sex in polygynous ungulates: a case study of bighorn sheep. Behav Ecol 16:274–279

Boulet M, Olsen P, Cockburn A, Newgrain K (2001) Parental investment in male and female offspring by the Peregrine Falcon, *Falco peregrinus*. Emu 101:95–103

Clutton-Brock TH (1986) Sex ratio variation in birds. Ibis 128:317–329

Clutton-Brock TH, Albon SD, Guinness FE (1986) Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim Behav 34:460–471

Daan S, Dijkstra C, Weissing FJ (1996) An evolutionary explanation for seasonal trends in avian sex ratio. Behav Ecol 7:426–430

Dijkstra C, Daan S, Buker JB (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. Funct Ecol 4:143–147

Don RH, Cox PT, Wainwright BJ, Baker K, Mattick JS (1991) "Touchdown" PCR to circumvent spurious priming during gene amplification. Nucleic Acids Res 19:4008

Festa-Bianchet M (1996) Offspring sex ratio studies of mammals—Does publication depend upon the quality of the research or the direction of the results? Ecoscience 3:42–44

Festa-Bianchet M, Jorgenson JT, Réale D (2000) Early development, adult mass and reproductive success in bighorn sheep. Behav Ecol 11:633–639

Fletcher KL, Hamer KC (2004) Offspring sex ratio in the common tern *Sterna hirundo*, a species with negligible sexual size dimorphism. Ibis 146:454–460

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

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

Gonzáles-Solis J (2004) Sexual size dimorphism in northern giant petrels: ecological correlates and scaling. Oikos 105:247–254

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

Hasselquist D, Kempenaers B (2002) Parental care and adaptive brood sex ratio manipulation in birds. Philos Trans R Soc Lond B 357:363–372

Heinsohn R, Legge S, Barry S (1997) Extreme bias in sex allocation in Eclectus parrots. Proc R Soc Lond B 264:1325–1329

Hewison AJM, Gaillard J-M (1999) Successful sons or advantaged daughters? The Trivers–Willard model and sex-biased maternal investment in ungulates. Trends Ecol Evol 14:229–234

Jouventin P, Lequette B, Dobson FS (1999) Age-related mate choice in the wandering albatross. Anim Behav 57:1099–1106

Kölliker M, Heeb P, Werner I, Mateman AC, Lessells CM, Richner H (1999) Offspring sex ratio is related to male body size in the great tit (*Parus major*). Behav Ecol 10:68–72

Komdeur J (1998) Long-term fitness benefits of egg sex modification by the Seychelles warbler. Ecol Lett 1:56–62

Komdeur J, Daan S, Tinbergen J, Mateman C (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525

Krackow S (1995) Potential mechanisms for sex ratio adjustment in mammals and birds. Biol Rev 70:225–241

Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE (1999a) Population density affects sex ratio variation in red deer. Nature 399:459–461

Kruuk LEB, Clutton-Brock TH, Rose KE, Guiness FE (1999b) Early determinants of lifetime reproductive success differ between the sexes in red deer. Proc R Soc Lond B 266:1655–1661

Nager RG, Monaghan P, Griffiths R, Houston D, Dawson R (1999) Experimental demonstration 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

Pen I, Weissing FJ, Daan S (1999) Seasonal sex ratio trend in the European kestrel: an evolutionarily stable strategy analysis. Am Nat 153:384–397

Pike TW, Petrie M (2003) Potential mechanisms of avian sex manipulation. Biol Rev 78:553–574

R Development Core Team (2003) R: a language and environment for statistical computing Vienna: R Foundation for Statistical Computing

Radford AN, Blakey JK (2000) Is variation in brood sex ratios adaptive in the great tit (*Parus major*)? Behav Ecol 11:294–298

Sasvári L, Hegyi Z (2001) Condition-dependent parental effort and reproductive performance in the white stork *Ciconia ciconia*. Ardea 89:281–291

Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. Funct Ecol 15:203–210

Sheldon BC (1998) Recent studies of avian sex ratios. Heredity 80:397–402

Sheldon BC, West SA (2004) Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. Am Nat 163:40–54

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 79:90–91

Van Shaik CP, Hrdy SB (1991) Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. Am Nat 138:1555–1562

Wang H, Qi M, Cutler AJ (1993) A simple method of preparing plant samples for PCR. Nucleic Acids Res 21:4153–4154

Wauters LA, Decrombrugghe SA, Nour N, Matthysen E (1995) Do female roe deer in good condition produce more sons than daughters. Behav Ecol Sociobiol 37:189–193

Weatherhead PJ, Teather KL (1991) Are skewed fledgling sex ratios in sexually dimorphic birds adaptive? Am Nat 138:1159–1172

Weimerskirch H, Lys P (2000) Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. Polar Biol 23:733–744

Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. Biol Conserv 79:257–270

Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V (1997b) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology 78:2051–2063

Weimerskirch H, Barbraud C, Lys P (2000) Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. Ecology 81:309–318

Weimerskirch H, Lallemand J, Martin J (2005) Population sex ratio variation in a monogamous long-lived bird, the wandering albatross. J Anim Ecol 74:285–291

West SA, Reece SE, Sheldon BC (2002) Sex ratios. Heredity 88:117–124

Westerdahl H, Bensch S, Hansson S, Hasselquist B, Von Schantz T (1997) Sex ratio variation among broods of great reed warblers *Acrocephalus arundinaceus*. Mol Ecol 6:543–548

Whittingham LA, Dunn PO (2000) Offspring sex ratios in tree swallows: females in better condition produce more sons. Mol Ecol 9:1123–1129

Williams TD (1979) The question of adaptive sex ratio in outcrossed vertebrates. Proc R Soc Lond B 205:567–580