Ibis (2002), **144**, 000–000

Sex ratio in relation to timing of breeding, and laying sequence in a dimorphic seabird

ALBERTO VELANDO[1], JEFF. GRAVES[2] & JOSE E. ORTEGA-RUANO[2,3]
[1]*Departamento de Ecoloxía e Bioloxía Animal, Campus Lagoas-Marcosende. Universidade de Vigo, 36200 Vigo. Spain*
[2]*School of Environmental and Evolutionary Biology, University of St Andrews, St Andrews KY16 9TS, UK*

When the cost of rearing sons and daughters differs and the subsequent survival and reproductive success of one sex is more dependent than the other, on the amount of parental investment, adult females tend to produce more chicks of the more dependent sex if the females are in good condition themselves. One method of varying the total investment in each sex is through modifying the sex ratio of offspring produced. This study shows that in broods of European Shags *Phalacrocorax aristotelis*, the sex ratio varied with laying date. Presumably in this species, the lifetime reproductive success of males is more dependent on the level of parental investment. Early breeders are in better condition, the brood sex ratio of early broods was male biased (0.63), while that of late broods was female biased (0.36). The overall difference in sex ratio found between early and late nests could be attributed to manipulation of sex in the first laid egg. In early broods, 77% of the first hatched chicks were male but only 30% of the first hatched chicks in late broods were male. The sex combination of the first two chicks in a brood significantly affected growth as measured by asymptotic mass.

Sex allocation theory predicts that females with the capacity to adjust the sex ratio in accordance with their potential fitness gain of each sex should be fitter than females lacking that ability (Trivers & Willard 1973, Frank 1990). Recently, adaptive sex ratio manipulation has been found in several studies of birds (Ellegren *et al.* 1996, Komdeur 1996, Svensson & Nilsson 1996, Heinsohn *et al.* 1997, Komdeur *et al.* 1997, Sheldon *et al.* 1999). In size-dimorphic birds, the largest sex is also the most expensive to rear (Fiala & Congdon 1983, Teather 1987, Wiebe & Bortolotti 1992, Anderson *et al.* 1993, Riedstra *et al.* 1998; but not in all species, see Newton 1978, Richter 1983), and consequently the survival and reproductive success of the largest sex could be more dependent on the amount of parental resources. Females may tend to produce the largest sex when they are in good nutritional condition and/or there is high food availability.

Moreover, in bird species that are sexually dimorphic in size, the sex distribution within a brood can affect the growth of competing siblings (Bortolotti 1986, Schaadt & Bird 1993). Bortolotti (1986) reported that in Bald Eagles *Haliaetus leucocephalus* the frequency of different sex combinations in asynchronously hatching broods was not random, and that the sex combination affected competition for food and chick mortality. Dzus *et al.* (1996) in the same population showed that the interaction between the sex of a chick and its position in the hatching sequence varied with food supply. Apparently, no further research has been carried out to date in birds on the interaction between growth, sex and hatching order (Mock & Parker 1997).

We examined the sex ratio of the European Shag *Phalacrocorax aristotelis*, a seabird in which males are approximately 20% heavier than females during the breeding season (Cramp & Simmons 1977). Better quality males (in size, experience and age) breed earlier, are more successful, and obtain the best breeding sites and mates (Potts *et al.* 1980, Aebischer 1985, Aebischer *et al.* 1995, Velando 1997). Females may seek males that are of better quality than their social mates for extra-pair fertilizations (Houtman 1992, Graves *et al.* 1993a, Hasselquist *et al.* 1996, Kempenaers *et al.* 1997). Male reproductive performance varies seasonally, and the number of extra-pair

---

*Corresponding author.
Email: avelando@uvigo.es

[3]Present address: Departamento de Psicobiología. Universidad Autónoma de Madrid, 28049 Madrid, Spain.

copulations a male has is negatively correlated with his laying date, and positively with his size (Graves *et al*. 1993a, Graves & Ortega Ruano unpubl. data). Aebischer (1993) found that the effect of laying date was due to the poorer quality of late breeders.

The aim of this study was to investigate departures of sex ratio from unity in the European Shag. Assuming that timing of breeding has an influence on the future reproductive performance of male offspring we predict that the sex ratio in early pairs should be biased toward males. Emlen (1997) suggested that females could control the sex ratio by absorbing eggs. Thus, birds that lay clutches of more than one egg should bias the sex of the first laid egg and then let the rest of the clutch be determined randomly. If female European Shags control the sex ratio as a seasonal response, according to the hypothesis, the sex biases on early broods should be due to a bias of the first laid egg.

Finally, the European Shag has intense intrabrood competition (Amundsen & Stokland 1988, Velando 1997). If sexes are not affected equally by sibling competition, or are not equally effective at competing with a sibling of the opposite sex, the cost of raising sexually size-dimorphic offspring may depend partly on the sex composition of the brood. Parents may therefore manipulate the sex ratio of their brood to optimize the combination of sexes to maximize their fitness (Bortolotti 1986). With this in mind, we examine the effects of sex and hatching sequence on chick growth.

METHODS

Study populations and field work

The study was carried out in 1996 in two subcolonies of a colony on the Cíes Islands (42°15′04″N, 8°53′30″, Galicia, NW Spain). The laying date was recorded for each of 56 nest sites, which were first marked in 1994, and the eggs marked according to the laying sequence. These nests produced 130 chicks in 1996. The hatching date of each chick was recorded during daily visits and time of hatching either recorded directly or estimated from the timing of hatching stages (according to Stokland & Amundsen 1988).

Hatching sequence was determined by marking the bill with indelible coloured markers while the chicks were hatching or immediately after hatching. At 5 days of age each chick was tagged on the tarsus with a velcro strip that identified hatching order by colour. These strips were enlarged to fit tarsus size as the chicks grew. At 15 days of age, the chicks were ringed with numbered metallic rings provided by the Dirección General de Conservación de la Naturaleza (Ministerio de Medio Ambiente, Spain).

The chicks were weighed with a spring balance (to the nearest gram for birds weighing up to 100 g, to the nearest 5 g between 100 and 300 g, and to the nearest 10 g between 300 and 2000 g). The length of the exposed culmen, head length and tarsus length were measured to the nearest 0.1 mm. The flattened wing chord was measured to the nearest 1 mm. Chicks were measured about seven times during the first 15 days from hatching and subsequently every 4 days until fledging. Blood samples of 43 chicks in this population were taken when the chicks were 20 days old.

Sex-identification and calculation of sex ratio

We used an RNA probe prepared from pSPT 19.6 derivative of Jeffreys' minisatellite probe 33.6 for DNA fingerprinting to sex the chicks (Graves *et al*. 1992, 1993a). Forty-three chicks were sexed using the presence or absence of a female-specific band at 27 kb (Graves *et al*. 1993b). The morphometric measurements of these chicks were used to produce a discriminant function that correctly classified the sex of 100% of the chicks starting at 30 days of age (Velando *et al*. 2000). The remaining chicks ($n = 84$) were sexed using this analysis.

Data analysis

Deviations in sex ratio from 1 : 1 (males to females) were tested with two-tailed binomial tests. The growth of body mass was fitted to a logistic model that provided a better fit than the Gompertz and von Bertalanffy models (see Ricklefs 1968 for a description of the different models). The logistic model has the following form: $y = A/(1 + Bekt)$, where y is the mass, A is the asymptotic value, B the intercept at origin, k the growth constant (day–1) and t the age (day). The growth constant (k) is representative for the overall growth rate and for the duration of the growth period (Ricklefs 1968, Richner 1991). The growth equations for mass were fitted for individual chicks. All logistic models were carried out by nonlinear model estimation with the Levenberg-Marquardt algorithm (Noruš is 1994).

A principal component analysis was carried out using the correlation matrix of the morphometric variables including all the data obtained for each chick studied. The first principal component extracted (PC1) accounts for 97% of the variance, with an eigenvalue of 3.89 and a Pearson correlation coefficient of 0.995 with culmen length, 0.998 with head length, 0.946 with wing length and 0.950 with tarsus length. PC1 is a synoptic descriptor of body size and its increase during the first 40 days of life was fitted with a cubic polynomial for individual chicks. The asymptotic value of body mass (*g*), growth constant (*k*) and the body size (PC1) were compared with a MANOVA, analysing the sums of squares using the Type I method for unbalanced data (Noruš is 1994). In this analysis we used the sex, the position in the brood, laying date and the combinations of sexes in the broods according to their position as factors.

RESULTS

Seasonal variations in sex ratio

Broods laid on or before the median laying date (18 March) had a significantly higher proportion of males than broods laid after this date (all broods, *n* = 51: Mann–Whitney test *Z* = 3.01, *n* = 51, *P* = 0.007; Broods where all eggs were sexed: *Z* = 2.68, *n* = 38, *P* = 0.010, Fig. 1).

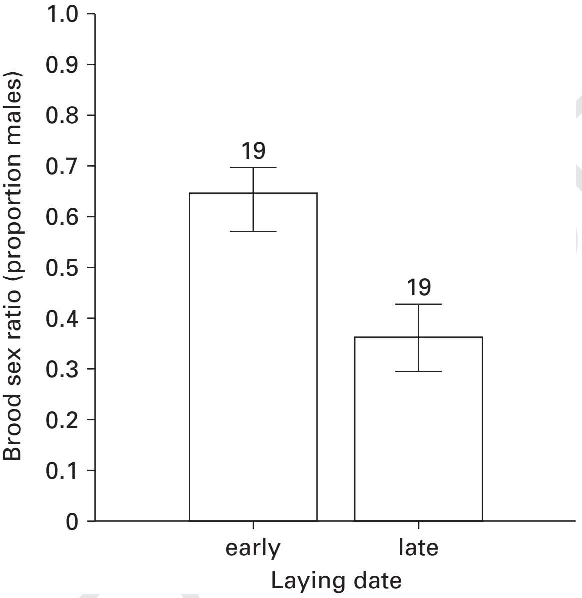

Figure 1. Brood sex ratio (M/M + F) for those three-chick broods where all the eggs laid were sexed (mean ± SE, number of broods above the bars). Early laying date was prior to or including 18 March and late after that date.

Effect of laying order on the sex of chicks

The sex ratio for the different positions in the hatching order differed significantly from parity (*n* = 127 chicks, G = 8.57, *df* = 3, *P* = 0.035). The first laid egg was more often male than female, the second was more often female, and the third slightly male biased (Fig. 2). The fourth was female in all four cases. The difference in sex ratio between the early and late nests was due to the first egg (Fig. 2). In early nests 77% of the first laid eggs were male, but in late nests only 30% were male (Fisher exact test *P* = 0.002).

The sex combination of the first two chicks depended on the laying date (*n* = 45 nests, G = 14.57, *df* = 3, *P* = 0.002, Fig. 3). In 40% of the early broods the first two laid eggs were both males but only 5% in the late nests (Fig. 3). The sequence first female then male was the most uncommon combination and occurred in only 8% (2/25) of early broods.

Effect of hatching order in the brood and sex on chick growth

The asymptotic body mass, growth constant (*k*) and body size (PC1 at age of 40 days, see Methods) of the first two chicks were analysed with a MANOVA using sex, the position in the brood (1st or 2nd), laying date (early and late) and the combinations of sexes in the broods according to their position (M–M, F–F, M–F, F–M) as factors (see Table 1). The descriptive data for all parameters are given in Velando *et al.* (2000). The MANOVA showed significant differences in chick mass in relation to sex, position in the brood and sex combination (Fig. 4), but the interaction between them was not significant. Male chicks were approximately 17% heavier than female chicks. The interaction between sex combination and laying date was significant. The growth constant was affected only by the position in the brood (Table 1); second chicks had a higher growth constant than first chicks. There was a significant effect of sex on body size (PC1), but there was no significant effect of sex combination, position and laying date or two–way interactions (Table 1).

A *post hoc* analysis (LSD) indicated that the asymptotic mass of males hatching second was significantly lower than male chicks that hatched first (mean difference 5% of body mass [83 g]). Moreover, the *post hoc* analysis showed that the combination F–M produced the smallest chicks of both sexes (Fig. 4). Using residuals to control for the effects of sex on mass, there was a significant correlation

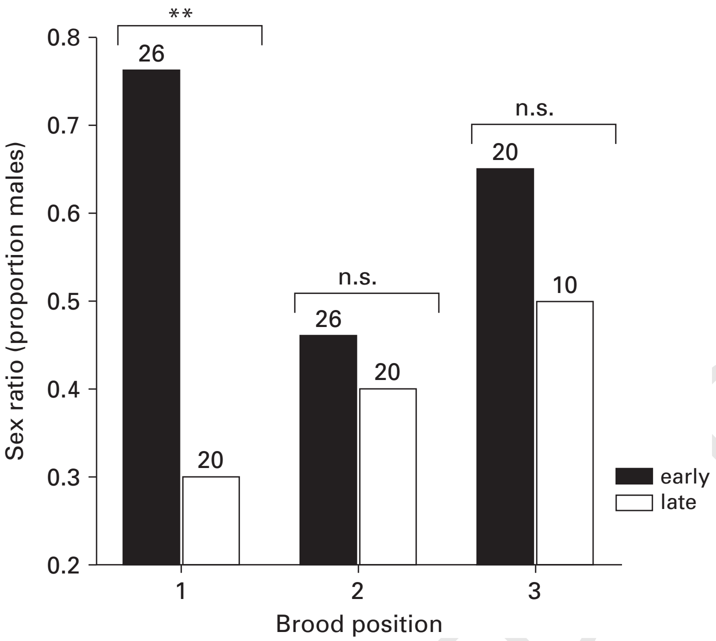

Figure 2. Sex ratio (M/M + F) in the nests according to hatching position in broods and laying date (number of chicks above the bars). Symbols above the bars denote the significant differences of each position between early and late broods (Fisher's exact test, n.s. $P > 0.05$, $^{**}P < 0.01$).

between the frequency of each combination in the population and deviation from the mean asymptotic mass of the nestlings (Spearman's rank correlation, $r_s = 1.0$, $n = 4$, $P = 0.04$). Thus the most frequent strategy was the one that produced the heaviest chicks (Figs 3 & 4).

DISCUSSION

Seasonal changes in sex ratio

There was a significant difference between early and late nests in the sex ratio, with earlier broods containing more males. Seasonal variations in sex ratio have also been found in the Common Grackle *Quiasculus quiscua* (Howe 1977), Great Tit *Parus major* (Lessells *et al.* 1996) and some birds of prey (Dijkstra *et al.* 1990, Olsen & Cockburn 1991, Zijlstra *et al.* 1992, Daan *et al.* 1996, Tella *et al.* 1996; but see Sayce & Hunt 1987, Wiebe & Bortolotti 1992).

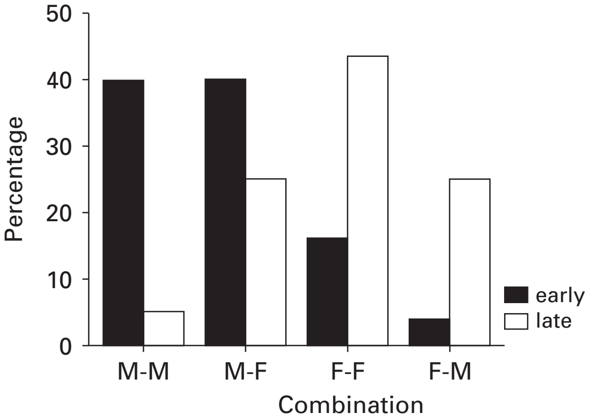

Figure 3. Percentage of clutches with different sex combinations in early (filled bars, $n = 25$) or late broods (open bars, $n = 20$).

Brood sex ratio in birds may be linked to maternal body condition and food availability (Patterson & Emlen 1980, Meathrel & Ryder 1987, Wiebe & Bortolotti 1992, Dzus *et al.* 1996, Komdeur 1996, Appleby *et al.* 1997, Komdeur *et al.* 1997, Kilner 1998, Torres & Drummond 1999). In sexually size-dimorphic species, females produce the cheaper sex when conditions are poor and/or when little food is available (Meathrel & Ryder 1987, Patterson & Emlen 1980, Wiebe & Bortolotti 1992, Dzus *et al.* 1996, Torres & Drummond 1999). In the European Shag, females that lay early are in better body

Table 1. Results of a four-way MANOVA comparing the asymptotic mass, growth constant and body size (PC1) of the first two chicks with the factors brood position (1st or 2nd), sex combination (M–M, F–F, M–F, F–M), laying date (early or late) and sex. Significant results are shown in bold type ($P < 0.05$).

		Dependent variables					
		Asymptotic mass (g)		Growth contant (*k*)		Body size (PC1)	
Source of variation	*df*	*F*	*P*	*F*	*P*	*F*	*P*
Sex	1	47.03	**< 0.001**	2.74	0.103	9.01	**0.004**
Sex combination	3	19.13	**< 0.001**	1.67	0.183	2.62	0.058
Position	1	4.45	**0.039**	4.30	**0.042**	2.08	0.154
Laying date	1	0.21	0.652	0.47	0.495	0.31	0.578
S × SC	1	0.61	0.439	0.07	0.790	0.49	0.484
S × L	1	0.65	0.423	0.56	0.456	0.56	0.456
SC × P	1	0.19	0.663	1.34	0.251	1.71	0.195
SC × L	3	3.26	**0.027**	0.73	0.538	1.05	0.373
P × L	1	3.673	0.060	1.51	0.223	3.41	0.070
residual	60						

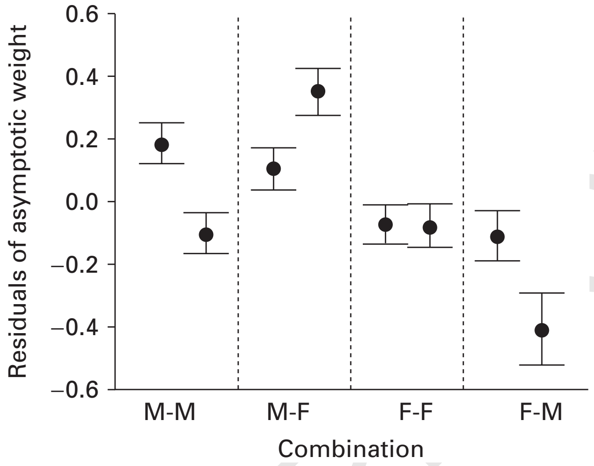

Figure 4. Effects of sex combination for the first two chicks on chick growth, measured as standardized residuals (mean ± SE) of the asymptotic body mass of the chicks in each sex combination. Residuals were obtained from the logistic fit of mass for all the chicks of each sex.

condition (Coulson *et al.* 1969) and thus would be able to invest more in the more expensive males.

Early nesting pairs may also have more food available. (In the Cíes Islands there are significant seasonal changes in European Shag diet and in the abundance of some prey, but no data exist on the effects on availability of food for the Shags in this colony [Velando 1997, Velando & Freire 1999, Velando *et al.* 1999].) Moreover, laying date is negatively correlated with male age, size, quality and extra-pair paternity (Aebischer *et al.* 1995, Velando 1997). The male, besides being the more demanding sex, is also the sex with the greater variability in reproductive success (Graves *et al.* 1993a). Females that mate with males of higher quality should bias the sex ratio in favour of males, owing to their greater future reproductive success.

Male lifetime reproductive success may also be related to age at the first breeding attempt (Daan *et al.* 1996). In the European Shag, the best time to have male chicks is early in the season, as they are more likely to be reproductively successful than males hatched later. Chicks hatched earlier in the season survive better (Harris *et al.* 1994) and are more dominant (Velando 2000). Dominance and body condition are crucial in male competition for breeding sites, rather than for females, and therefore in male recruitment. Male European Shags arrive at the colony before the females. At this time there is severe competition between males for breeding sites (Snow 1963, Potts *et al.* 1980, Aebischer *et al.* 1995, Velando 1997). Producing male-biased broods early in the season would seem to be adaptive because early breeders are more likely to be able to afford the cost and can increase their reproductive success by producing successful males.

Sex ratio and brood sequence

In birds, females are the heterogametic sex, and the presence or absence of the W chromosome is not determined until the final meiotic division, which occurs only hours before ovulation (Romanoff 1960). Several mechanisms have been suggested to explain the sex ratio variation in birds, including

Table 2. Predominant sex of the first egg in different species of birds. The larger sex in each species is given (M male, F female and – indicates a monomorphic species) and whether a significant difference was found in the sex of the first laid egg (*$P < 0.05$, **$P < 0.01$)

Species	Sex of 1st laid egg	*P*	Larger sex	Reference
Agelaius phoeniceus	M	n.s.	M	Weatherhead (1983)
	M	*	M	Fiala (1981)
Anser caerulescens	M	**	M	Ankney (1982)
	1:1	n.s	M	Cooke & Harmsen (1983)
Xanthocephalus xanthocephalus	M	*	M	Patterson & Emlen (1980)
Larus delawarensis	M	**	M	Ryder (1983)
Haliaetus leucocephalus	F	*	F	Bortolotti (1986)
good year		**	F	Dzus *et al.* (1996)
bad year			M	
Falco tinnunculus	F	**	F	Dijkstra *et al.* (1990)
Falco peregrinus	F	n.s	F	Olsen & Cockburn (1991)
Parabuteo unicintus	M	**	F	Bednarz & Hayden (1991)
Circus pygargus	F	**	F	Leroux & Bretagnolle (1996)
Phalacrocorax aristotelis	M	*	M	This study
early		**	M	This study
late			F	
Taeniopygia guttata	M	**	–	Clotfelter (1996)
	F	*	–	Kilner (1998)

maternal control of chromosomal segregation, specific destruction of eggs and differential growth of follicles by hormonal interaction (Godfray & Harvey 1986, Krakow 1995). Emlen (1997) suggested that the females could control the sex ratio by absorbing (or dump laying) an egg of the 'inappropriate' sex. If meiosis is random, a female would have to skip 0, 1 and 2 days on average to achieve a 50, 75 and 87% probability of producing each egg of the desired sex. Emlen suggested that birds that lay clutches of more than one egg should bias the sex of the first laid egg and then let the rest of the clutch be determined randomly.

Our results suggest that the sex of the chick is linked to its position in the brood sequence. Studies of the Seychelles Warbler *Acrocephalus sechellensis* have shown the most extreme known sex ratio variations (Komdeur *et al.* 1997), but this species lays only one egg. In the European Shag we found marked variations in the sex of the first laid egg: 77% of the first eggs in early nests were male, but only 30% were male in the late nests. The first chick was biased to the larger sex. This seems to be the case in most other studies of sex ratio in size-dimorphic birds (Table 2). Only one out of 12 studies found the opposite trend (Bednarz & Hayden 1991). However, the trend may depend on food availability. Dzus *et al.* (1996) found that in the Bald Eagle the first hatched egg was female biased when food was abundant. In years when food was less abundant, the first hatched egg was male biased and there was an overall male bias in the sex ratio of the hatched chicks. The existence of different strategies in different conditions might explain why a bias in the sex ratio of the brood order has not generally been found in other species (e.g. Cooke & Harmsen 1983).

We found that, in the European Shag, the sex combination affected the asymptotic mass of the chicks. Bortolotti (1986) suggested that Bald Eagle chicks in the combination male–female (the least commonly occurring combination of two chicks) there is a negative interaction with growth. Chicks in this combination develop less favourably than in the others. In conditions of food stress chicks in male–female broods are more likely to show siblicide (Dzus *et al.* 1996).

European Shag chicks compete aggressively within the brood (Snow 1963). Differences in the asymptotic mass of chicks between different sex combinations could affect the intensity of sibling competition. Thus, sibling competition could be less intense in M–F broods and most intense in F–M broods (Bortolotti 1986). In some species asynchronous hatching reduces the competition between siblings by producing a stable dominance hierarchy within the brood (Mock & Ploger 1987). A reversal in the dominance hierarchy might cause a period of intense competition. However, Drummond *et al.* (1991) and Drummond & Osorno (1992) found that the hierarchy between sibling Blue-footed Boobies *Sula nebouxii* was established during the early stages of growth and that an initially submissive chick did not later become dominant, even if it was of the larger sex. This species usually only lays two eggs with very pronounced hatching asynchrony of about 4 days. In European Shags the first two chicks hatch almost synchronously, with 24 h difference at the most, so we might expect to see greater competition. If the first-hatched chick is female, a second-hatched male will overtake her, and there will be a period of intense competition between them. Experimental studies that manipulate the sex combinations within the hatching order are needed to explain sex biases in hatching sequence (Myers 1978).

We thank M. Alvarez, B. Gamallo, L. Sampedro and M.J. Briones for their assistance in collecting data in the Cíes Islands. Professor A. Jeffreys kindly gave us the human minisatellite probes, and D. Parkin, J. Wetton and R. Carter provided the RNA probes and gave considerable advice. K. Lessells, J. Freire, G.R. Bortolotti, C. Macias Garcia and one anonymous referee commented extensively on earlier drafts of this manuscript. A.V. was funded by grant of Universidade de Vigo.

REFERENCES

Aebischer, N.J. 1985. Aspects of biology of the Shag (*Phalacrocorax aristotelis*). PhD Thesis, University of Durham.

Aebischer, N.J. 1993. Immediate and delayed effects of a gale in late spring on the breeding Shags *Phalacrocorax aristotelis. Ibis* **135**: 225–232.

Aebischer, N.J., Potts, G.R. & Coulson, J.C. 1995. Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. *Ibis* **137**: 19–28.

Amundsen, T. & Stokland, J.G. 1988. Adaptive significance of asynchronous hatching in the shag: a test of the brood reduction hypothesis. *J. Anim. Ecol.* **57**: 329–334.

Anderson, D.J., Reeve, J., Gomez, J.E.M., Weathers, W.W., Houston, S., Cunningham, H.V. & Bird, D.M. 1993. Sexual size dimorphism and food requirements of nestling birds. *Can. J. Zool.* **71**: 2541–2545.

Ankney, C.D. 1982. Sex ratio varies with egg sequence in Lesser Snow Geese. *Auk* **99**: 662–666.

Appleby, B.M., Petty, S.J., Blakey, J.K., Rainey, P. & MacDonald, D.W. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? *Proc. R. Soc. Lond. B.* **264**: 1111–1116.

Bednarz, J.C. & Hayden, T.J. 1991. Skewed brood se ratio and sex-biased hatchling sequence in Harris Hawks. *Am. Nat.* **137**: 116–132.

Bortolotti, G.R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* **127**: 495–507.

Clotfelter, E.D. 1996. Mechanisms of facultative sex-ratio variation in Zebra Finches (*Taeniopygia guttata*). *Auk* **113**: 441–449.

Cooke, F. & Harmsen, R. 1983. Does sex ratio vary with egg sequence in Lesser Snow Geese? *Auk* **100**: 215–217.

Coulson, J.C., Potts, G.R. & Horobin, J. 1969. Variation in the eggs of the Shag (*Phalacrocorax aristotelis*). *Auk* **86**: 232–245.

Cramp, S. & Simmons, K.E.L. 1977. *The Birds of the Western Paleartic*, Vol. I. Oxford: Oxford University Press.

Daan, S., Dijkstra, C. & Weissing, F.J. 1996. An evolutionary explanation for seasonal trends in avian sex ratios. *Behav. Ecol.* **7**: 426–430.

Dijkstra, C., Daan, S. & Buker, J.B. 1990. Adaptive seasonal variation in the sex-ratio of Kestrel broods. *Func. Ecol.* **4**: 143–147.

Drummond, H. & Osorno, J.L. 1992. Training siblings to be submissive: dominance between booby nestlings. *Anim. Behav.* **44**: 881–893.

Drummond, H., Osorno, J.L., Torres, R., García Chavelas, C. & Larson, H.M. 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. *Am. Nat.* **138**: 623–641.

Dzus, E.H., Bortolotti, G.R. & Gerrard, J.M. 1996. Does sex-biased hatching order in bald eagles vary with food resources? *Ecoscience* **3**: 252–258.

Ellegren, H., Gustafsson, L. & Sheldon, B.C. 1996. Sex ratio adjustment in relation to parental attractiveness in a wild bird population. *Proc. Nat. Ac. Sci.* **93**: 11723–11728.

Emlen, S.T. 1997. When mothers prefer daughters over sons. *Trends Ecol. Evol.* **12**: 291–292.

Fiala, K.L. 1981. Sex ratio constancy in the red-winged blackbird. *Evolution* **35**: 898–910.

Fiala, K.L. & Congdon, J.D. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* **64**: 642–647.

Frank, S.A. 1990. Sex allocation theory for birds and mammals. *Ann. Rev. Ecol. Syst.* **21**: 13–55.

Godfray, H.C.J. & Harvey, P.H. 1986. Bald eagle sex ratios: ladies come first. *Trends Ecol. Evol.* **1**: 56–57.

Graves, J., Hay, R.T., Scallan, M. & Rowe, S. 1992. Extra-pair paternity in the shag, *Phalacrocorax aristotelis* as determined by DNA. *J. Zool.* **226**: 399–408.

Graves, J., Ortega-Ruano, J. & Slater, J.B. 1993a. Extra-pair copulations and paternity in shags: do females choose better males? *Proc. R. Soc. Lond. B* **253**: 3–7.

Graves, J., Ortega-Ruano, J. & Slater, J.B. 1993b. Sex ratio of chicks in the Shag *Phalacrocorax aristotelis* determined by a female-specific band in DNA fingerprinting. *Ibis* **135**: 470–472.

Harris, M., Russell, S.M. & Wanless, S. 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *J. Avian Biol.* **25**: 268–274.

Hasselquist, D., Bensch, S. & Von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**: 229–232.

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

Houtman, A.M. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. *Proc. R. Soc. Lond. B* **249**: 3–6.

Howe, H.F. 1977. Sex ratio adjustment in the common grackle. *Science* **198**: 744–747.

Kempenaers, B., Verheyen, G.R. & Dhondt, A.A. 1997. Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics and offspring quality. *Behav. Ecol.* **8**: 481–492.

Kilner, R. 1998. Primary and secondary sex ratio manipulation by zebra finches. *Anim. Behav.* **56**: 155–164.

Komdeur, J. 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc. Lond. B* **263**: 661–666.

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.

Krakow, S. 1995. Potential mechanisms for sex ratio adjustment in mammals and birds. *Biol. Rev.* **70**: 744–745.

Leroux, A. & Bretagnolle, V. 1996. Sex ratio variations in broods of Montagu's Harriers *Circus pygargus*. *J. Avian Biol.* **27**: 63–69.

Lessells, C.M., Mateman, A.C. & Visser, J. 1996. Great Tit hatchling sex ratios. *J. Avian Biol.* **27**: 135–142.

Meathrel, C.E. & Ryder, J.P. 1987. Sex ratios of ring-billed gulls in relation to egg size, egg sequence and female body condition. *Col. Waterbird* **10**: 72–77.

Mock, D.W. & Parker, G.A. 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.

Mock, D.W. & Ploger, B.J. 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Anim. Behav.* **35**: 150–160.

Myers, J.H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *Am. Nat.* **112**: 381–388.

Newton, I. 1978. Feeding and development of Sparrowhawk *Accipiter nisus* nestlings. *J. Zool. Lond.* **184**: 465–487.

Noru is, M.J. 1994. *SPSS Advanced Statistics-Professional Statistics 6.1*. Chicago: SPSS Inc.

Olsen, P.D. & Cockburn, A. 1991. Female-based sex allocation in Peregrine Falcons and other raptors. *Behav. Ecol. Sociobiol.* **28**: 417–423.

Patterson, C.B. & Emlen, J.M. 1980. Variation in nestling sex ratios in the yellow-headed blackbird. *Am. Nat.* **115**: 743–747.

Potts, G.R., Coulson, J.C. & Deans, I.R. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *J. Anim. Ecol.* **49**: 465–484.

Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex-ratio theory: Does sex-specific growth contribute to balanced sex-ratios? *Funct. Ecol.* **5**: 19–28.

Richter, H. 1983. Balanced sex-ratios in dimorphic altricial birds: The contribution of specific growth dynamics. *Am. Nat.* **121**: 158–171.

Ricklefs, R. 1968. Patterns of growth in birds. *Ibis* **110**: 419–451.

Riedstra, B.C., Dijkstra, C. & Daan, S. 1998. Daily energy expenditure of male and female Marsh Harrier nestlings. *Auk* **115**: 635–641.

Romanoff, A.L. 1960. *The Avian Embryo*. New York: Macmillan.

Ryder, J.P. 1983. Sex ratio and egg sequence in Ring Billed Gulls. *Auk* **100**: 726–729.

Sayce, J.R. & Hunt, G.L. Jr. 1987. Sex ratios of prefledging Western Gulls. *Auk* **104**: 33–37.

Schaadt, C.P. & Bird, D.M. 1993. Sex-specific growth in Ospreys: the role of sexual size dimorphism. *Auk* **110**: 900–910.

Sheldon, B.C., Andersson, S., Griffith, S.C., Örnborg, J. & Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**: 874–877.

Snow, B. 1963. The behaviour of the shag. *Br. Birds* **56** (77–103): 164–186.

Stokland, J.N. & Amundsen, T. 1988. Initial size hierarchy in broods of the Shag: relative significance of egg size and hatching asynchrony. *Auk* **105**: 308–315.

Svensson, E. & Nilsson, J.Å. 1996. Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond. B* **263**: 357–361.

Teather, K. 1987. Intersexual differences in food consumption by hand-reared Great-tailed Grackle (*Quiasculus mexicanus*) nestlings. *Auk* **104**: 635–639.

Tella, J.L., Donazar, J.A., Negro, J.J. & Hiraldo, F. 1996. Seasonal and interannual variations in the sex-ratio of Lesser Kestrel *Falco naumanni* broods. *Ibis* **138**: 342–345.

Torres, R. & Drummond, H. 1999. Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* **118**: 16–22.

Trivers, R.L. & Willard, D.E. 1973. Natural selection and paternal ability to vary the sex ratio of offspring. *Science* **179**: 90–92.

Velando, A. 1997. Ecología y comportamiento del cormorán moñudo *Phalacrocorax aristotelis* en las Islas Cíes y Ons. PhD Thesis, Universidad de Vigo.

Velando, A. 2000. The importance of the hatching date on dominance of young shags. *Anim. Behav.* **60**: 181–185.

Velando, A. & Freire, J. 1999. Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain). *Mar. Ecol. Prog. Series* **188**: 225–236.

Velando, A., Graves, J. & Freire, J. 2000. Sex-specific growth in the European Shag *Stictocarbo aristotelis*, a seabird with size dimorphism. *Ardea* **88**: 127–136.

Velando, A., Ortega-Ruano, J.C. & Freire, J. 1999. Chick mortality in European Shag *Stictocarbo aristotelis* related to food-limitations during adverse weather events. *Ardea* **87**: 51–59.

Weatherhead, P.J. 1983. Secondary sex ratio adjustment in red-winged blackbirds. *Behav. Ecol. Sociobiol.* **12**: 57–61.

Wiebe, K.L. & Bortolotti, G.R. 1992. Facultative sex ratio manipulation in American kestrels. *Behav. Ecol. Sociobiol.* **30**: 379–386.

Zijlstra, M., Daan, S. & Bruinenberg-Rinsma, J. 1992. Seasonal variation in the sex ratio of Marsh Harrier *Circus aeroginosus* broods. *Funct. Ecol.* **6**: 553–559.

Received 18 February 2000; revision accepted 22 February 2001

Author Query Form

Journal: IBIS

Article: 002

Dear Author,

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof.

Many thanks for your assistance.

Query Refs.	Query	Remarks
1	**Krackow 1995** has been changed to **Krakow 1995** so that this citation matches the list	
2	**Paterson & Elmen 1980** has been changed to **Patterson & Emlen 1980** so that this citation matches the list	