

Roxana Torres · Hugh Drummond

## Variably male-biased sex ratio in a marine bird with females larger than males

Received: 3 February 1998 / Accepted: 12 September 1998

**Abstract** When the costs of rearing males and females differ progeny sex ratios are expected to be biased toward the less expensive sex. Blue-footed booby (*Sula nebouxi*) females are larger and roughly 32% heavier than males, thus presumably more costly to rear. We recorded hatching and fledging sex ratios in 1989, and fledging sex ratios during the next 5 years. In 1989, the sample of 751 chicks showed male bias at hatching (56%) and at fledging (57% at ~90 days). Fledging sex ratios during the five subsequent reproductive seasons were at unity (1 year) or male-biased, varying from 56% to 70%. Male bias was greater during years when mean sea surface temperature was warmer and food was presumably in short supply. During two warm-water years (only) fledging sex ratio varied with hatching date. Proportions of male fledglings increased with date from 0.48 to 0.73 in 1994, and from 0.33 to 0.79 in 1995. Similar results were obtained when the analysis was repeated using only broods with no nestling mortality, suggesting that the overall increase in the proportion of males over the season was the result of sex ratio adjustments at hatching. The male-biased sex ratio, and the increased male bias during poor breeding conditions supports the idea that daughters may be more costly than sons, and that their relative cost increases in poor conditions.

**Key words** Interannual variation · Seasonal variation · Sex ratio · Size dimorphism · *Sula nebouxi*

### Introduction

Fisher (1930) suggested that total investment by parents in offspring of each sex should be equal at the end of

parental care. If the sexes are equally costly to produce, this will lead to a 1:1 ratio in the population; if the sexes differ in cost, the least expensive sex should be over-produced (Maynard Smith 1980; Charnov 1982). A sex ratio close to unity could simply be the result of Mendelian segregation; thus, species where daughters and sons differ in cost are needed to test the predictions of sex ratio theory. Here, we report a male-biased sex ratio at hatching and at fledging, and variation in fledging sex ratios among years and over the reproductive season in the blue-footed booby (*Sula nebouxi*), a species with sexual size dimorphism: the females are larger. Evidence of parental adjustment was also sought by examining sex ratio in relation to parents' reproductive experience and laying sequence.

In dimorphic species, the larger sex is assumed to be more costly because of its presumed higher food requirements (Fiala 1981; Slagsvold et al. 1986; Teather 1987; Richner 1991; but see Richter 1983); hence, over-production of the smaller sex is expected according to Fisher's hypothesis. However, the influence of size dimorphism on the relative cost of sons and daughters is not clear. Greater expenditure on the larger sex has been reported in some species but not in others (Clutton-Brock 1991). For example, in mammals greater expenditure on offspring of the larger sex occurs in the red deer (*Cervus elaphus*, Clutton-Brock et al. 1981), the California sea lion (*Zalophus californianus*, Ono and Boness 1996), and the American bison (*Bison bison*, Wolff 1988); yet no differences were found in the Antarctic fur seal (*Arctocephalus gazella*, Lunn and Arnould 1997), the fallow deer (*Dama dama*, Birgersson and Ekvall 1997), or the grey seal (*Halichoerus grypus*, Smiseth and Lorentsen 1995).

In birds, differential provisioning of sons and daughters when the sexes differ in size has rarely been found (Slagsvold et al. 1986; Teather and Weatherhead 1988; Stamps 1990), but laboratory evidence suggests that the larger sex has greater energetic needs (Fiala 1981; Fiala and Congdon 1983; Teather and Weatherhead 1988; Anderson et al. 1993) or food consumption

R. Torres (✉) · H. Drummond  
Instituto de Ecología,  
Universidad Nacional Autónoma de México, A.P. 70–275,  
México D.F., 04510, México  
e-mail: rtorres@miranda.ecologia.unam.mx, Fax: +52-5-6161976

(Teather 1987; Frumkin 1988; but see Newton 1978; Newton and Marquiss 1979; Anderson et al. 1993). Furthermore, few studies have found a preponderance of the cheaper sex in offspring of size-dimorphic birds (e.g., *Quiscalus quiscula*, Howe 1977; *Quiscalus mexicanus*, Teather and Weatherhead 1989; *Larus fuscus*, Griffiths 1992; review in Clutton-Brock 1986), and the evidence so far is scarcely consistent with Fisherian expectations (Weatherhead and Teather 1991). For instance, where females are larger, sex ratios at fledging are unbiased in some species (*Accipiter nisus*, Newton and Marquiss 1979; *Haliaeetus leucocephalus*, Bortolotti 1986; *Falco tinnunculus*, Dijkstra et al. 1990), vary between years in other species (*Circus c. cyaneus*, Picozzi 1980; *Aquila chrysaetos*, Edwards et al. 1988; *Parabuteo unicinctus*, Bednarz and Hayden 1991), and are male-biased in yet other species (*Falco sparverius*, Wiebe and Bortolotti 1992; *Circus aeruginosus*, Zijlstra et al. 1992).

These sex ratios apparently inconsistent with Fisherian expectations may be related to variations in parental or ecological conditions (Trivers and Willard 1973; Charnov 1982; Frank 1990; Komdeur et al. 1997). If reproductive conditions are favourable, differential cost of sons versus daughters may be trivial; if conditions deteriorate the difference may increase. Consistent with this suggestion, underweight female ring-billed gulls (*Larus delawarensis*), in a year of presumably low food availability laid smaller clutches of lighter eggs, and overproduced daughters, the smaller sex (Meathrel and Ryder 1987).

Blue-footed booby female adults are roughly 32% heavier than males (Castillo and Chavez-Peón 1983; Nelson 1978). Both parents raise from one to three chicks, which hatch at intervals of roughly 4 days (Drummond et al. 1986). At hatching, nestlings of both sexes are similar in size and mass (ulna:  $23.1 \pm 0.8$  mm for males and  $23.3 \pm 0.7$  mm for females,  $t = 0.19$ ,  $df = 20$ ,  $P = 0.84$ ; mass:  $45.5 \pm 5.64$  g for males and  $42.7 \pm 5.4$  g for females,  $t = 1.01$ ,  $df = 15$ ,  $P = 0.32$ ; Drummond et al. 1991). However, females grow faster, and before the end of parental care, reach a higher asymptotic size and mass than males (ulna:  $200 \pm 2.65$  mm, range 191–207 mm,  $n = 325$ , for males and  $220 \pm 3.43$  mm, range 213–233 mm,  $n = 247$ , for females; Drummond et al. 1991).

We used mean sea surface temperature (SST) as an index of breeding conditions; SSTs are good indicators of sea productivity at all trophic levels (Barber and Chavez 1983; Schreiber and Schreiber 1984). For instance, in the states of Sinaloa and Nayarit, México, catch-by-effort from thread herring (*Opisthonema spp.*) landings approximately follow broad SST variations, decreasing in warm-water years and increasing in cool-water years (Ruiz and Lyle 1992); and herrings are the most common prey in the boobies' diet (H. Drummond and I. Calixto, unpublished work). Accordingly, blue-footed boobies at Isla Isabel did not produce a single chick during the El Niño event of 1992, a warm-water year, compared with 551 fledglings produced in the same

area in 1994 (García-Cerecedo and Saavedra-Sordo 1997). Also, at Isla Isabel SST increases over the reproductive season and it is negatively correlated with the number of chicks that fledge (García-Cerecedo and Saavedra-Sordo 1997).

Our aim was to test predictions from sex ratio theory and assess the effect of breeding conditions on progeny sex ratios. Assuming that females cost more than males, and that the greater cost of the larger sex increases as breeding conditions deteriorate, we predicted: (1) a male-biased sex ratio at fledging, due to male-bias at hatching or greater mortality of female nestlings, (2) increase in male bias at fledging in years of poor breeding conditions and with hatching date, and (3) greater production of females by parents with more reproductive experience (more fledglings produced during previous years).

Finally, last-hatched chicks of blue-footed boobies are subordinate and suffer greater mortality than their siblings (facultative siblicidal brood reduction; Drummond et al. 1991). If brood reduction is a mechanism that may serve to equalise investment in sons and daughters (Slagsvold 1990), we predicted that (4) parents should bias mortality toward (costly) females by hatching a higher proportion of females in final position than in earlier positions in the hatching sequence.

---

## Materials and methods

This study was conducted on Isla Isabel, Nayarit, México, during 1989–1995. Intensive data collection in 1989 covered most of the breeding season (12 February to 23 July) and approximately 80% of the nests in the colony, including dense and sparse nesting areas. The data were collected by daily nest inspections at two areas, Las Monas and Costa Fragatas, roughly 200 m apart (map in Osorio-Beristain and Drummond 1993). All sites with eggs or chicks (nests) were marked with numbered flags and chicks were banded when 3 days old using coloured wire to differentiate hatching order, and with individually numbered plastic bands when they were 7 days old. Survival of chicks was recorded daily until fledging (when plumage development is completed, mean age = 86 days for males, and 90.5 days for females; Drummond et al. 1991). Ulna and culmen length were measured at fledging, when these structures approximate adult sizes (Drummond et al. 1991), and fledglings were permanently marked with individually numbered steel bands.

Sex of all hatched chicks was determined in a total of 400 broods (751 chicks). Of the 751 chicks used in analyses, the 572 fledglings were sexed by the length of the ulna at fledging, when males and females have reached a non-overlapping bimodal asymptote (Drummond et al. 1991). Additionally, 207 banded chicks from our sample were sexed again by their voice (males whistle and females grunt; Nelson 1978) when they bred in the colony 4 years later; only one case (0.5%) did not agree with morphometric determination at fledging.

The 179 chicks that died before fledging and whose bodies were recovered were sexed in the field by inspection of gonadal morphology. To test the reliability of the field sexing, gonads were preserved in karnovsky (pH 7.3) when chicks were < 30 days old, and in 10% formalin when chicks were older. Tissue differentiation of gonads of a sample of 100 chicks of all ages (1–90 days) was examined under the microscope. Males were identified by the presence of seminiferous cords and scattered Leydig cells; females showed sex cords and/or follicles containing germ cells undergoing the prophase of the first meiotic division (Drummond et al. 1991).

Sex identification by tissue differentiation in the laboratory, and inspection of gonadal morphology in the field agreed in 99 of 100 cases.

A further 116 broods were eliminated from our analyses because we were unable to sex all members of each brood (145 out of 243 chicks could not be sexed). Excluded broods were considered to be an unbiased sample with respect to sex, as we are unaware of any likely source of bias: in 14 broods 14 chicks lost their band, in 4 broods 7 chicks did not fledge before data recording ended, in 5 broods 6 fledglings could not be sexed, in 34 broods 42 corpses were in advanced state of decomposition when recovered, and in 59 broods 76 corpses were not found. Chicks whose bodies were not found were on average 9.52 days old ( $\pm 9.68$  days,  $n = 61$ ; 15 chicks were of unknown age), and were probably victims of predation by the milk snake (*Lampropeltis triangulum*; Drummond et al. 1991). Since males and females do not differ in mass when younger than 12 days (Drummond et al. 1991), predation risk is probably similar for both sexes during their first 10 days of life. Sex ratios of excluded broods were similar to unity at hatching and fledging: 51% ( $n = 98$ ,  $G = 0.08$ ,  $df = 1$ ,  $P = 0.77$ ) and 55% ( $n = 65$ ,  $G = 0.74$ ,  $df = 1$ ,  $P = 0.38$ ) males, respectively.

Data recording began some time after the start of incubation in the colony, thus original clutch size of some broods is unknown. Eggs are sometimes lost, mainly to predation by gulls (*Larus heermanni*). However, there is no reason to expect that egg loss to predation might affect one sex more than the other, and eggs of this species are similar in mass and size regardless of their position in the laying sequence (Castillo and Chavez-Peón 1983).

The ages of the 440 chicks included in the analyses that had already hatched at the beginning of the study were estimated from the average hatching interval of 4 days (Drummond et al. 1986) when we knew the hatching date of any chick in the brood, or from the population's average age of fledging (Drummond et al. 1991). Their estimated age was  $13.4 \pm 9.4$  days (range, 1–54 days).

Protocols for 1990–1995 were similar to 1989, except that survival was recorded every 3 days until most of the chicks in the colony were 30 days old, and thereafter every 6 days until all chicks fledged. Because nest visits were less frequent than in 1989, corpses from chicks that died before fledging were not recovered and could not be sexed. As an indicator of breeding conditions (food availability) in each year, we used the mean SST ( $^{\circ}\text{C}$ ) at roughly 9 km around Isla Isabel from January to July, which is the egg-laying and chick-raising period (SSTs are calculated by direct and satellite measurements; data from the University of Columbia, benno@Ideo.columbia.edu).

To test for an association between sex ratio and hatching date, and between sex ratio and parents' reproductive experience, we used logistic regression models (GLMs) with a logit link function and binomial distribution of error (Crawley 1993). To avoid pseudoreplication by treating individual chicks as independent units, we used the brood as the unit of analysis (Lessells et al. 1996).

Broods from 1990 were excluded from the analysis of sex ratio and hatching date because of small sample size ( $n = 54$  broods).

We analysed the effect of reproductive experience on progeny sex ratios in a year of presumably good breeding conditions (1989, a cool-water year) and in a year of poor breeding conditions (1994, a warm-water year). Herring catch-by-effort (tons of fresh fish/ship) in the south of the Gulf of Baja California, México, was 4,333 tons in 1989, and 2,864 tons in 1994 (PESCA 1995). Also, these two years were selected because large samples of banded parents were available. Our index of reproductive experience was the total number of chicks fledged by banded parents between 1982 and 1993 (the years with available data). When both parents of a brood were banded, the parent with greater reproductive experience was used.

Williams' correction was used for all the  $G$ -tests of goodness of fit and independence (Sokal and Rohlf 1981).

## Results

### Sex ratio at hatching and at fledging

The sex ratios of 300 broods from Las Monas and 100 broods from Costa Fragatas did not differ at hatching ( $n = 751$ ,  $G = 1.28$ ,  $df = 1$ ,  $P = 0.25$ ), or at fledging ( $n = 572$ ,  $G = 1.10$ ,  $df = 1$ ,  $P = 0.29$ ), so data from both sites were pooled for analyses. Hatching failure in our 1989 sample was high. Of 230 two-egg clutches, 33% failed to hatch one egg; and of 135 three-egg clutches, 33% and 11% failed to hatch one and two eggs respectively. Differential mortality of the sexes during incubation could not be detected, because a non-destructive method for sexing an egg is not available (Fiala 1981; Griffiths 1992). To screen for any bias arising from differential hatching failure of males and females, we report sex ratio of all broods and also of only broods where all eggs hatched.

The expected overall male-biased sex ratio was confirmed. Using all broods in our 1989 sample, the proportion of males was 56% at hatching, and 57% at fledging (Table 1a). More males were produced in all clutch sizes, but the bias towards males was significant only in three-egg clutches (Table 1a). Similar results were obtained when only broods where all the eggs hatched were included (Table 1b).

**Table 1** Hatching and fledging sex ratios (proportion of males) according to clutch size in 1989. Analyses using **a** all broods, and **b** only broods where all eggs hatched are reported ( $df = 1$  in all  $G$ -tests, significance criterion = 0.05 in all the power analyses)

Eggs	Hatchlings					Fledglings				
	Ratio	$n$	$G$	$P$	Power	Ratio	$n$	$G$	$P$	Power
<b>a</b> All broods										
1	0.63	35	2.30	0.13	0.20	0.65	29	2.79	0.09	0.20
2	0.54	385	2.82	0.09	0.25	0.54	299	2.43	0.12	0.20
3	0.58	331	7.87	0.005		0.59	244	7.25	0.007	
Total	0.56	751	11.53	0.0007		0.57	572	10.66	0.001	
<b>b</b> Broods where all eggs hatched										
1	0.63	35	2.30	0.13	0.20	0.65	29	2.79	0.09	0.20
2	0.57	310	6.26	0.01		0.58	243	6.94	0.008	
3	0.56	228	3.44	0.06	0.33	0.57	169	4.32	0.03	
Total	0.57	573	11.48	0.0007		0.59	441	13.49	0.0002	

Pre-fledging mortality did not differ for male and female chicks. Overall, 23% of 422 males and 25% of 329 females died during the nestling period ( $G = 0.38$ ,  $df = 1$ ,  $P = 0.53$ ).

### Sex ratios at fledging among years

Sex ratios at fledging varied among years. From 1989 to 1995, excluding 1992 (an El Niño year when no chicks fledged), more males than females fledged in all years except one, and the size of the bias towards males varied among years ( $G = 17.42$ ,  $df = 5$ ,  $P = 0.003$ ; Table 2).

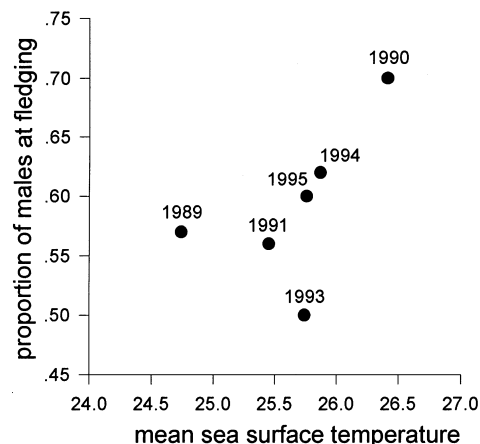
As predicted, the proportion of male fledglings each year increased with the mean SST (chi-square test for trend,  $\chi^2 = 6.73$ ,  $df = 1$ ,  $P = 0.009$ ; Fig. 1), reaching 70% in the warmest year.

### Sex ratio and hatching date

Sex ratios at hatching in 1989 did not show a significant variation over the season ( $\chi^2 = 0.10$ ,  $df = 1$ ,  $P = 0.75$ ). However, at fledging sex ratios increased with hatch date in some years but not in others. In 1989 and 1991, the proportion of male fledglings did not vary

**Table 2** Sex ratios (proportion of males) at fledging over six reproductive seasons ( $df = 1$  in all  $G$ -tests)

Year	Sex ratios at fledging			
	Ratio	$n$	$G$	$P$
1989	0.57	572	10.66	0.001
1990	0.70	93	15.05	0.0001
1991	0.56	352	6.02	0.01
1993	0.50	366	0.01	0.92
1994	0.62	551	31.41	0.0001
1995	0.60	189	7.27	0.007



**Fig. 1** Proportion of males at fledging and mean sea surface temperature (SST, °C) during 1989–1995. 1992 was excluded because no fledglings were produced during that El Niño year. Mean SST for 1992 was 26.48°C

**Table 3** Variation of sex ratios at fledging with hatching date and clutch size in 6 reproductive seasons. Analyses were carried out using logistic regression models. The significance of each explanatory variable was assessed by the change in deviance when the variable was included last in the model, and the change in deviance is distributed asymptotically as  $\chi^2$ . The interaction term and departure from linearity (quadratic term) in each year were also tested but none was significant. In 1995, broods of three eggs were too few ( $n = 7$ ) to be included in the analysis; 1990 was excluded from the analysis because of small sample size

Year	Broods	Hatching date			Clutch size		
		$\chi^2$	$df$	$P$	$\chi^2$	$df$	$P$
1989	376	0.80	1	0.37	1.70	2	0.42
1991	258	1.90	1	0.16	1.20	2	0.54
1993	301	3.10	1	0.08	0.90	2	0.63
1994	371	9.80	1	0.001	2.60	2	0.27
1995	145	9.81	1	0.001	0.89	1	0.34

over the season (Table 3), but during 1994 and 1995 (years with high mean SST) the proportion of males increased with hatching date (Table 3, Fig. 2). In 1993, another warm year, a similar effect was evident but fell short of significance (Table 3). Significant effects were large: the probability of producing a male fledgling increased over the season from 0.48 to 0.73 in 1994 (Fig. 2a), and from 0.33 to 0.79 in 1995 (Fig. 2b).

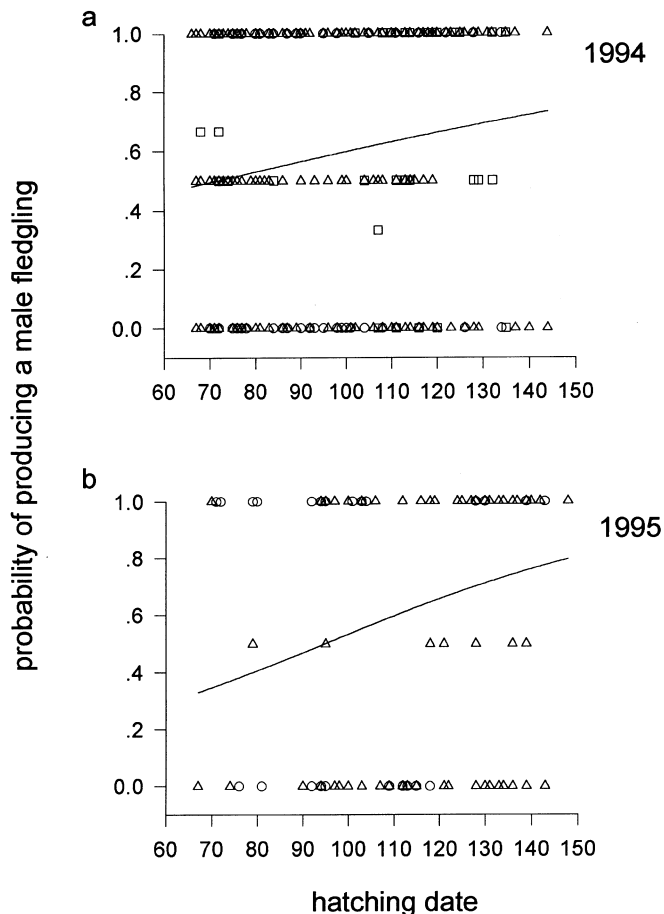
Similar results were obtained for 1994 and 1995 when only broods where all chicks fledged were used: the proportion of male fledglings increased with hatching date in both years (1994,  $\chi^2 = 9.00$ ,  $df = 1$ ,  $P = 0.002$ ; 1995,  $\chi^2 = 9.34$ ,  $df = 1$ ,  $P = 0.002$ ).

Thus, the expected greater production of male fledglings over the season was supported during the two warmest water years (mean SST) in our sample.

### Sex ratio and reproductive experience

There was no association between parents' reproductive experience (number of fledglings produced in the 11 preceding years) and progeny sex ratio in either of the two years analysed; a cool-water year with relatively abundant food (1989), and a warm-water year with relatively scarce food (1994). In 1989, the proportion of daughters that 50 banded parents produced was independent of parents' reproductive experience, both at hatching ( $\chi^2 = 0.26$ ,  $df = 1$ ,  $P = 0.61$ ) and at fledging ( $\chi^2 = 0.68$ ,  $df = 1$ ,  $P = 0.41$ ). Likewise, when breeding date was controlled, sex ratios did not vary with parents' reproductive experience, either at hatching ( $\chi^2 = 0.06$ ,  $df = 1$ ,  $P = 0.81$ ), or at fledging ( $\chi^2 = 0.02$ ,  $df = 1$ ,  $P = 0.86$ ).

In 1994, the proportion of daughters that 181 banded parents produced at fledging was independent of parents' reproductive experience ( $\chi^2 = 0.11$ ,  $df = 1$ ,  $P = 0.74$ ). Similarly, parents with different reproductive experience did not differ in their progeny sex ratios when breeding date was accounted for ( $\chi^2 = 0.86$ ,  $df = 1$ ,  $P = 0.35$ ).



**Fig. 2** Sex ratio variation over the season for **a** 1994 ( $r = 0.14$ ,  $P = 0.006$ ), and **b** 1995 ( $r = 0.21$ ,  $P = 0.009$ ). Analyses were performed using logistic regressions. Probability of producing a male =  $\exp(A + \beta \times \text{date}) / 1 + \exp(A + \beta \times \text{date})$ . The estimated terms in the exponential equations were: 1994,  $A = -0.987$ , and  $\beta = 0.0138$ ; 1995,  $A = -2.426$ , and  $\beta = 0.0256$ . Sample sizes were 59 one-egg clutches (circles), 272 two-egg clutches (triangles), and 40 three-egg clutches (squares) in 1994; 30 one-egg clutches, and 115 two-egg clutches in 1995. Hatching date 70 = 11 March. For visual clarity, data were grouped by days in the figure, but not for statistical analyses

### Sex ratio and hatching sequence

The relationship between sex ratio and hatching sequence within a brood was determined for 1989 broods of two and three chicks where all eggs of the clutch hatched. The expected greater proportion of females in the last position of the hatching sequence was not found. In 155 two-egg broods, similar proportions of females were produced in first and second positions in the hatching sequence: 43% and 43% at hatching ( $n = 310$ ,  $G = 0.00$ ,  $df = 1$ ,  $P = 1.00$ ), and 43% and 40% at fledging ( $n = 243$ ,  $G = 0.19$ ,  $df = 1$ ,  $P = 0.66$ ), respectively.

In 76 three-egg broods, the proportions of females hatched in first (49%) and third (50%) positions were similar ( $n = 152$ ,  $G = 0.02$ ,  $df = 1$ ,  $P = 0.87$ ); however, a smaller proportion of females hatched in second position (33%) than in final position (50%) within these broods ( $n = 152$ ,  $G = 4.60$ ,  $df = 1$ ,  $P = 0.03$ ). At

fledging, the proportion of females in final position (42%) did not differ from the proportion of females in first (51%,  $n = 111$ ,  $G = 0.91$ ,  $df = 1$ ,  $P = 0.34$ ) and second positions in the hatching sequence (34%,  $n = 107$ ,  $G = 0.68$ ,  $df = 1$ ,  $P = 0.40$ ).

### Discussion

The male-biased sex ratio found in the blue-footed booby seems to support Fisher's hypothesis, assuming females are more expensive to produce than males. In 1989 this male-biased sex ratio was evident at hatching, and no subsequent adjustment through differential mortality by sex was found overall. There are few reports of biased avian sex ratios at hatching (Gowaty and Lennartz 1985; Lessells et al. 1996; Komdeur et al. 1997), and it has been argued that hatching sex ratios of birds are fixed at unity (Charnov 1982; Clutton-Brock 1986; Weatherhead and Teather 1991). However, evidence of biased sex ratios at hatching may be scarce simply because so few data have been obtained; newly hatched birds are difficult to sex (though this is rapidly changing with the development of molecular techniques for sex determination; Griffiths 1992; Lessells et al. 1996; Komdeur et al. 1997).

Mechanisms for biasing the sex ratio at conception have not been identified for birds, but plausible suggestions include non-random segregation of sex chromosomes, and earlier or faster growth of ovarian follicles that will produce one sex (Howe 1977; Ankney 1982; Ryder 1983; Dijkstra et al. 1990; Gowaty 1991; Krackow 1995). However, even if the sex ratio at conception is close to unity, selective absorption or abortion, or differential mortality during incubation of one sex, could produce a biased sex ratio at hatching (Emlen 1997). In fact, in poultry chickens (*Gallus domesticus*), sex ratio variation of embryos seems to be related to length of incubation, with females showing greater mortality under pre-hatching stress (Landauer 1967). At present, we have no data to evaluate how blue-footed boobies are biasing the sex ratio at hatching, and there are virtually no data for other wild bird species.

Assuming 1989–1995 is a representative period, this population overproduces males. Furthermore, increased male bias during years of inferior breeding conditions is consistent with daughters being more costly to produce than sons: in response to food shortage parents may hatch fewer daughters or relative mortality of daughters may increase. In fact, among last-hatched chicks from late broods (chicks undergoing especially poor conditions), females do indeed suffer greater mortality than males (Torres and Drummond 1997).

Likewise, the rise over the reproductive season in the proportion of male fledglings during warm-water years (1994–1995), suggests that under lower food supply the relatively high cost of the larger sex increases. Sex ratios at hatching were not determined in 1994 and 1995, thus we can not directly assess whether the higher sex ratios

at fledging in late broods were the result of a male-bias at hatching, and/or differential mortality by sex. However, when only broods with no mortality were used, the proportion of males increased with hatching date, in just the same way. This indicates that sex ratios were adjusted at or before hatching, to accommodate to deteriorating breeding conditions.

Variation in fledging sex ratios over the breeding season has been reported in other avian species (*Angelaius phoeniceus*, Blank and Nolan 1983; *Falco peregrinus*, Olsen and Cockburn 1991; *Falco tinnunculus*, Dijkstra et al. 1990; *Circus aeruginosus*, Zijlstra et al. 1992; *Parus major*, Lessells et al. 1996). We focused on testing predictions based on the assumption that females, because of their larger size, are more costly than males. However, daughters and sons may differ in their reproductive returns, and changes in parental investment or breeding conditions may affect the reproductive value of males and females differentially (Trivers and Willard 1973; Dijkstra et al. 1990). For example, the proportion of males in the European kestrel declines with hatching date, and early-born males, but not females, are more likely to breed as a yearling than later-born birds (Dijkstra et al. 1990). Furthermore, in species where only females breed at age 1 year, Zijlstra et al. (1992) suggested that only females born early in the season will have sufficient time to mature and reproduce as yearlings. In the blue-footed booby females breed significantly earlier than males (age at first reproduction  $3.6 \pm 0.90$ , range 1–6 years, for 21 females, and  $4.7 \pm 0.90$ , range 2–6 years, for 9 males; Osorio-Beristain and Drummond 1993). Total recruitment of the 225 males and 215 females from the cohorts of 1989–1994 suggests that early hatching confers on females a greater chance to breed when young than it does to males. Female early breeders included 3 that bred at age 1, and 15 that bred at age 2, and all 18 of these early breeders hatched during the first month of the reproductive season. In contrast, 3 males bred at age 1 and none at age 2, and all of these 3 males were born during the middle of the season. We suggest that in the blue-footed booby changes in breeding conditions over the season may differentially affect the reproductive value of daughters and sons, and that this difference may be due to their size dimorphism.

We did not find any evidence that reproductive experience affects the sex ratio that parents produced. Also blue-footed boobies did not show any clear association between sex and laying sequence that might further balance parental investment in each sex. However, even if there is no female-bias in the last position of the laying sequence, parental investment could still be equalised through differential mortality of the larger sex when last hatched (Slagsvold 1990). In our sample of two-egg broods, although similar proportions of females hatched in first and second positions, fewer females than males fledged when hatched last.

Because most of the biased sex ratios observed hitherto in dimorphic birds are the result of differential

mortality by sex, it has been argued that these biased ratios may simply be the result of non-adaptive greater mortality of the larger sex (Clutton-Brock 1986; Weatherhead and Teather 1991; Griffiths 1992). In the blue-footed booby, male-bias at hatching suggests that the sex ratio may have been adjusted by natural selection; however, we cannot exclude the possibility of differential mortality before hatching.

The male-biased sex ratio at hatching, the increase in the male bias during poor years, and the rise in the proportion of males over the season during poor years, all support the idea that daughters are more costly than sons. Although explanations for overall sex ratio variation in dimorphic species have usually focused on the assumption that the larger sex is more expensive to rear and/or suffers greater mortality, there are alternative explanations (not necessarily mutually exclusive; Frank 1990; Gowaty 1993). For example, Gowaty (1993) suggests that differences in natal dispersal by sex, and thus local resource competition between relatives (Clark 1978) may be an important selective force for adjusting the sex ratio. We need to measure differences between sons and daughters in their food requirements and post-fledging interactions with parents, as well as looking for differential effects of sons and daughters on parental survival and future reproduction, to clarify whether the observed male-biased sex ratio in the blue-footed booby is an adaptation to differential costs of sons and daughters during rearing or differential benefits after they become independent.

**Acknowledgements** We thank the Universidad Nacional Autónoma de México, the National Geographic Society (grant no. 3065-85 to HD), and the SIGMA-Xi (Grant-in-Aid to RT) for financial support. Permissions were provided by the Secretaría de Desarrollo Urbano y Ecología. Horacio Merchant Larios advised and supported the laboratory sex determination of nestlings; Pablo Navarro greatly helped with the field work; Exequiel Ezcurra and Arturo Flores Martínez helped with statistical analyses; Constantino Macías García, César Domínguez, Patty Gowaty, Ken Yasukawa and Steven Orzack made useful comments on an early draft. We especially thank the fishermen of San Blás, Camichín and Teacapán for their generous support of the project.

## References

- Anderson DJ, Reeve J, Martinez Gomez JE, Weathers WW, Hutson S, Cunningham HV, Bird DM (1993) Sexual size dimorphism and food requirements of nestling birds. *Can J Zool* 71:2541–2545
- Ankney CD (1982) Sex ratio varies with egg sequence in lesser snow geese. *Auk* 99:662–666
- Barber R, Chavez F (1983) Biological consequences of El Niño. *Science* 222:1203–1210
- Bednarz JC, Hayden TJ (1991) Skewed sex ratio and sex-biased hatching sequence in Harris's hawks. *Am Nat* 137:116–132
- Birgersson B, Ekvall K (1997) Early growth in male and female fallow deer fawns. *Behav Ecol* 8:493–499
- Blank JL, Nolan V (1983) Offspring sex ratio in red winged blackbirds is dependent on maternal age. *Proc Natl Acad Sci USA* 80:6141–6145
- Bortolotti GR (1986) Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am Nat* 127:495–507
- Castillo A, Chavez-Peón A (1983) Ecología reproductiva e influencia del comportamiento en el control del número de crías

- en el bobo de patas azules, *Sula nebouxii* en la Isla Isabel, Nayarit. Bch thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México
- Charnov E (1982) The theory of sex allocation. Princeton University Press, Princeton
- Clark A (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165
- Clutton-Brock TH (1986) Sex ratio variation in birds. *Ibis* 120: 317–329
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Clutton-Brock TH, Albon SD, Guinness FE (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489
- Crawley MJ (1993) GLIM for ecologists. Blackwell, Oxford
- Dijkstra C, Daan S, Buker JB (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. *Funct Ecol* 4:143–147
- Drummond H, Gonzalez E, Osorno JL (1986) Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behav Ecol Sociobiol* 19:365–372
- Drummond H, Osorno JL, Torres R, García-Chavelas C, Merchant Larios H (1991) Sexual size dimorphism and sibling competition: implications for avian sex ratios. *Am Nat* 138:623–641
- Edwards TC, Collopy MW, Steenhof K, Kochert MN (1988) Sex ratios of fledging golden eagles. *Auk* 105:793–796
- Emlen ST (1997) When mothers prefer daughters over sons. *Trends Ecol Evol* 12:291–292
- Fiala KL (1981) Reproductive cost and the sex ratio in red-winged blackbirds. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior. Chiron, New York, pp 198–214
- Fiala KL, Congdon LD (1983) Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* 64:642–647
- Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford
- Frank SA (1990) Sex allocation theory for birds and mammals. *Annu Rev Ecol Syst* 21:13–55
- Frumkin R (1988) Egg quality, nestling development and dispersal in the sparrowhawk (*Accipiter nisus*). PhD thesis, University of Oxford, Oxford
- García-Cerecedo MA, Saavedra-Sordo MT (1997) Variación interanual en el esfuerzo y éxito reproductivo del bobo de patas azules (*Sula nebouxii*) y sus implicaciones en la reducción facultativa de la nidada. Bch thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México
- Gowaty PA (1991) Facultative manipulation of sex ratios in birds, rare or rarely observed? In: Johnson RF (ed) Current Ornithology, vol 8. New York, pp 141–171
- Gowaty PA (1993) Differential dispersal, local resource competition and sex ratio variation in birds. *Am Nat* 141:263–280
- Gowaty PA, Lennartz MR (1985) Sex ratios of nestling and fledging red-cockaded woodpeckers (*Picoides borealis*) favor males. *Am Nat* 126:347–353
- Griffiths R (1992) Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. *Ibis* 134:237–244
- Howe HF (1977) Sex ratio adjustment in the common grackle. *Science* 198:744–745
- Komdeur J, Daan S, Timbergen 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
- Landauer W (1967) The hatchability of chicken eggs as influenced by environment and heredity (Monograph 1). Storrs CT. Agriculture Experiment Station, University of Connecticut
- Lessells CM, Mateman AC, Visser J (1996) Great tit hatchling sex ratios. *J Avian Biol* 27:135–142
- Lunn NJ, Arnould JPY (1997) Maternal investment in Arctic fur seals: evidence for equality in the sexes? *Behav Ecol Sociobiol* 40:351–362
- Maynard Smith J (1980) A new theory of sexual investment. *Behav Ecol Sociobiol* 7:247–251
- Meathrel CE, Ryder JP (1987) Sex ratios of ring-billed gulls in relation to egg size, egg sequence and female body condition. *Colonial Waterbirds* 10:72–77
- Nelson JB (1978) The Sulidae: gannets and boobies. Oxford University Press, London
- Newton I (1978) Feeding and development of sparrowhawk nestlings. *J Zool Lond* 184:465–487
- Newton I, Marquiss M (1979) Sex ratio among nestlings of the European sparrowhawk. *Am Nat* 113:309–315
- Olsen PD, Cockburn A (1991) Female-biased sex allocation in peregrine falcons and other raptors. *Behav Ecol Sociobiol* 28:417–423
- Ono KA, Boness DJ (1996) Sexual dimorphism in sea lion pups: differential maternal investment, or sex specific differences in energy allocation? *Behav Ecol Sociobiol* 38:31–41
- Osorio-Beristain M, Drummond H (1993) Natal dispersal and deferred breeding in the blue-footed booby. *Auk* 110:234–239
- PESCA (1995) Anuario Estadístico de Pesca 1994. Secretaría de Pesca Dirección General de Estadística e Informática, Mexico
- Picozzi N (1980) Food, growth, survival and sex ratio of nestling Hen harriers *Circus c. cyaneus* in Orkney. *Ornis Scand* 11:1–11
- 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 W (1983) Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am Nat* 121:158–171
- Ruiz A, Lyle L (1992) Fluctuaciones periódicas de la captura de sardina crinuda (*Opisthonema spp.*) en el Golfo de California, Cooperative Ocean Fisheries Investigations (CalCOFI), Univ. of California SCRIPPS, San Diego. 1972–1990. CalCOFI 33:124–129
- Ryder J (1983) Sex ratio and egg sequence in ring-billed gulls. *Auk* 1:726–729
- Schreiber RW, Schreiber EA (1984) Central Pacific seabirds and the El Niño Southern Oscillation 1982 to 1983: perspectives. *Science* 225:713–716
- Slagsvold T (1990) Fisher's sex ratio theory may explain hatching patterns in birds. *Evolution* 44:1009–1017
- Slagsvold T, Roskaft E, Engen S (1986) Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scand* 17:117–125
- Smiseth T, Lorentsen S (1995) Evidence of equal maternal investment in the sexes in the polygynous and sexually dimorphic grey seal (*Halichoerus grypus*). *Behav Ecol Sociobiol* 36:145–150
- Sokal RR, Rohlf FJ (1981) Biometry, 2d edn. Freeman, San Francisco
- Stamps JA (1990) When should avian parents differentially provision sons and daughters? *Am Nat* 135:671–685
- Teather KL (1987) Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. *Auk* 104:635–639
- Teather KL, Weatherhead PJ (1988) Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. *J Anim Ecol* 57:659–668
- Teather K, Weatherhead PJ (1989) Sex-specific mortality in nestling great-tailed grackles. *Ecology* 70:1485–1493
- Torres R, Drummond H (1997) Female biased mortality in nestlings 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
- Weatherhead PJ, Teather K (1991) Are skewed fledglings sex ratios in sexually dimorphic birds adaptive? *Am Nat* 138:1159–1172
- Wiebe KL, Bortolotti R (1992) Facultative sex ratio manipulation in American kestrels. *Behav Ecol Sociobiol* 30:379–386
- Wolff JO (1988) Maternal investment and sex ratio adjustment in American bison calves. *Behav Ecol Sociobiol* 23:127–133
- Zijlstra M, Daan S, Bruinenberg-Rinsma J (1992). Seasonal variation in the sex ratio of marsh harrier *Circus aeruginosus* broods. *Funct Ecol* 6:553–559