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Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby

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Sex allocation theory predicts that mothers in good condition should bias their brood sex ratio in response to the differential benefits obtained from increased maternal expenditure in sons and daughters. Although there is well-documented variation of offspring sex ratios in several bird species according to maternal condition, the assumption that maternal condition has different fitness consequences for male and for female offspring remains unclear. The blue-footed booby (*Sula nebouxii*) is a sexually size-dimorphic seabird, with females approximately 31% heavier than males. It has been reported that the sex ratio is male biased in years with poor feeding conditions, which suggests that either females adjust their sex ratio in accordance with their condition or that they suffer differential brood mortality before their sex can be determined. In this study I tested whether the condition of mothers affected their daughters' fitness more than their sons' fitness. I manipulated maternal investment by trimming the flight feathers and thereby handicapping females during the chick-rearing period. Adult females in the handicapped group had a poorer physical condition at end of chick growth, as measured by mass and by the residuals of mass on wing length compared to control birds. Female chicks were affected by the handicapping experiment, showing a lower mass and shorter wing length (reduced approximately 8% in both measures) than controls. However, this effect was not found in male chicks. Hatching sex ratios were also related to female body condition at hatching. The brood sex ratio of females in poor condition was male biased but was female biased for females in good condition. Overall, these results suggest that the variation in the sex ratio in blue-footed boobies is an adaptive response to the disadvantage daughters face from being reared under poor conditions. *Key words:* blue-footed boobies, maternal investment, physical condition, sex allocation, sex ratios, *Sula nebouxii*. *[Behav Ecol 13:443–449 (2002)]*

Parental investment directly affects offspring fitness in a number of ways: survival, mating success, and reproductive success (reviewed in Clutton-Brock, 1991). However, the fitness of one sex may be more heavily dependent than the other sex on the amount of parental investment. This is a fundamental assumption of sex allocation theory, which predicts that mothers should produce more offspring of the more dependent sex when resources are plentiful in order to maximize their own lifetime reproductive success (Charnov, 1982; Frank, 1990; Trivers and Willard, 1973).

In the last decade, studies involving sex ratio manipulation have been performed in several bird species (e.g., Bradbury and Blakey, 1999; Dijkstra et al., 1990; Ellegren et al., 1996; Heinsohn et al., 1997; Hörnfeldt et al., 2000; Kilner, 1998; Komdeur et al., 1997; Lessells et al., 1996; Ligon and Ligon, 1990; Nishiumi, 1998; Sheldon et al., 1999; Svensson and Nilsson, 1996), although in some species the assumptions of sex ratio theory may be invalid. Thus, for example, it has been reported in some mammalian species that female condition did not have different fitness consequences for producing sons or daughters (Lunn and Arnould, 1997; Sikes, 1996). Skewed sex ratios of offspring according to maternal condition and/or food availability in bird species has been well documented (e.g., Appleby et al., 1997; Bradbury and Blakey, 1998; Dzus et al., 1996; Kilner, 1998; Komdeur et al., 1997; Meathrel and Ryder, 1987; Nager et al., 1999; Paterson and Emlen, 1980; Torres and Drummond, 1999b; Whittingham and Dunn, 2000; Wiebe and Bortolotti, 1992). In contrast, the evidence that maternal condition has different fitness consequences for male and for female offspring is limited (Appleby et al., 1997; Kilner, 1998; Nager et al., 1999).

In some sexually size-dimorphic bird species, females produce the smaller sex when food availability is low (Dzus et al., 1996; Olsen and Cockburn, 1991; Paterson and Emlen, 1980; Torres and Drummond, 1999b; Wiebe and Bortolotti, 1992). This could be adaptive if the fitness of the larger sex is more affected by maternal condition than that of the smaller sex. It is generally assumed that the larger sex is more costly to produce than the smaller sex (Anderson et al., 1993; Krijgsveld et al., 1998; Stamps, 1990), although the relative cost of sons and daughters remains unclear. In dimorphic birds, greater energy demands and food consumption by the larger sex have been reported in some species (Anderson et al., 1993; Fiala and Congdon, 1983; Krijgsveld et al., 1998; Riedstra et al., 1998; Teather, 1987; Wiebe and Bortolotti, 1992), while other studies suggest that the members of both sexes have similar energy requirements but different resource allocation during growth (Newton, 1978; Richter, 1983; Torres and Drummond, 1999a).

The blue-footed booby (*Sula nebouxii*) is a sexually size-dimorphic seabird, with females approximately 31% heavier than males during the breeding season (Nelson, 1978; Velando, unpublished data). At hatching, nestlings of both sexes are similar in size and mass, but females grow significantly

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faster than males (Drummond et al., 1991). This is a good species in which to investigate the differential effects of maternal condition on chick growth because chick growth is highly dependent on maternal investment, and the amount of food given by females to the chicks is three times more than that given by males (Anderson and Ricklefs, 1992). In a recent study, Torres and Drummond (1999b) reported that fledging sex ratios are related to environmental conditions. Thus, in years with poor conditions, the sex ratio was male biased, which suggests that females adjust sex ratios in accordance with their condition. This adjustment will be adaptive if maternal condition has a greater effect on the fitness of daughters than of sons.

Blue-footed booby females typically spend a high proportion of time flying, making two long (4 h) pelagic foraging trips per day (Anderson and Ricklefs, 1992). The amount of investment by the female was manipulated by increasing the cost of flight. Studies in birds show that using such handicaps reduces the amount of parental care received by the chicks (Mauck and Grubb, 1995; Sæther et al., 1993; Slagsvold and Liefjeld, 1988, 1990; Wright and Cuthill, 1989). Investment in current reproduction should be balanced against the chances of reproducing in the future (Roff, 1992; Stearns, 1992). In long-lived species, current reproductive investment is more likely to be regulated by the impact of reproductive effort on the future survival of the parents (Linden and Møller, 1989), and it has been reported that seabirds have a fixed upper level of investment in their current reproduction (Mauck and Grubb, 1995; Sæther et al., 1993).

The aim of this study was to analyze the effect of increased flight costs of in blue-footed booby females. I predicted that (1) increased flight costs would result in decreased investment in the current offspring without any change in the body condition of adults; (2) reduced female investment would affect daughters more than sons because female nestlings grow faster and reach a higher asymptotic size and mass than male nestlings (Drummond et al., 1991), and their mortality is more related to food stress than that of males (Torres and Drummond, 1997); and (3) the sex ratio in blue-footed boobies would vary with female condition, and broods of females in good condition would be female biased if females have the capacity to adjust the sex ratio of their broods in accordance with the potential fitness gain for each sex.

MATERIALS AND METHODS

Study area

This study was conducted on Isla de Lobos de Tierra (06°28′ S, 80°50′ W) on the Peruvian coast during the summer of November 1998 to January 1999. Blue-footed boobies breed on the pampas or on the slopes and in the flat valleys. More than 10,000 pairs breed in Lobos de Tierra, which may be the world's largest colony of the species (Nelson, 1978). In one large colony (defined as a discrete nest aggregation), I used numbered stones to mark 30 nests, each with two eggs. The first chicks in each nest hatched between 1 and 12 December. I captured the female parents on the marked nests when the chicks were less than 7 days old. Adult boobies were captured early in the morning to avoid heat stress.

Experimental protocol

Ethical considerations were taken into account in the experiment design to minimize the damage caused by increasing flight costs while still eliciting a measurable response. The crucial decision was the choice of phenotypic manipulation that would increase the cost of flight. The energetic cost of flight in birds can be experimentally increased by adding mass or decreasing the wing span (Pennycuick, 1989). Adding mass can affect the bird's stability and drag, and if the individual is not recaptured the damage is permanent. The handicap produced by clipping feathers and thereby reducing the wing span disappears soon after the normal postbreeding moult and will have a less dramatic effect on flight (Cuthill, 1991; Mauck and Grubb, 1995).

Previous handicap studies on seabirds increased the cost of flight by 9–10% (e.g., Sæther et al., 1993; Mauck and Grubb, 1995; Weimerskirch et al., 1999), and in some of these studies also caused nest desertion of some adults (Sæther et al., 1993; Weimerskirch et al., 1999). Thus, if I used a similar increase, I could expect a proportion of handicapped adults to desert. To avoid desertion and to keep the number of subjects needed as low as possible (Still, 1982), I decided to increase the flight cost by approximately 5%. I cut each of the primary remiges 3 cm shorter, measuring from the tip and perpendicular to the long axis. Reducing the female wing span by 6 cm (average mass for a female is 1985 g of mass and average wing span of 154 cm) increased the cost of flight by approximately 5% (see Pennycuick, 1989, for calculations). Experimental manipulation was made at the early chick stage to control effects operating via eggs (see Nager et al., 2000).

Nests were divided randomly into two groups according to treatment. In 10 experimental nests the adult females were handicapped, and in 10 control nests the adult females were captured and handled but not handicapped. The handling time was similar in both groups of birds. The captured adults were ringed, measured (wing length and outer right rectrix), and weighed. I plucked the outer right rectrix (tail feather), thereby inducing the growth of a replacement. This allowed me to measure the nutritional condition of birds during the experiment (Grubb, 1989).

I weighed the chicks at 45 days of age with a spring balance and measured the wing length using the wing chord flattened method with a metallic ruler with a stop. Adults were recaptured and weighed when the chicks were 45–50 days old. Induced rectrix growth was measured, and an index of growth rate was obtained by dividing induced feather length by the original feather length and dividing again by the number of days between pulling and recapture (Mauck and Grubb, 1995). The residuals of the linear regression of body mass on wing length were used to avoid the effect of structural body size on body mass. The residuals obtained were standardized in a Z normal distribution.

Sex identification and sex ratio

Chicks were individually marked according to hatching sequence with indelible colored markers on their bills. When the birds were 10 days old, each one was tagged with a strip of Velcro on its tarsus and identified by a number on the strip. At the same age, I obtained a blood sample from each bird by puncturing the wing vein and transferring the blood in a capillary to a tube containing an equal volume of ethanol. Sex was determined through polymerase chain reaction (PCR) amplification of part of the *CHD* gene using primers P2 and P8 following Griffiths et al. (1998). PCR products were visualized and photographed under UV light. Two patterns were observed: males had one single band at approximately 370 bp, and females had a second additional band at approximately 390 bp. I confirmed the correspondence of these patterns to the sexes with four adult individuals (two females and two males that had been sexed by voice and eye examination: Nelson, 1978).

I sexed all chicks in the nests used for the experiment ($n = 20$), as well as in the remaining nests ($n = 10$). The pro-

Table 1

Indices of condition and body mass for control and handicapped blue-footed boobies recaptured at the end of the experiment

Variable	Control ($n = 9$)	Handicapped ($n = 9$)	t	p
Body mass (g)	2016 ± 22	1891 ± 45	2.49	.024
Body mass change (g)	11.11 ± 76.72	−172.44 ± 37.44	2.15	.047
Body condition	0.88 ± 0.21	−0.16 ± 0.21	2.44	.027
Body condition changes	0.57 ± 0.45	−0.57 ± 0.20	2.30	.039
Feather growth index	0.145 ± 0.056	0.122 ± 0.012	1.79	.090

Body condition (body mass relative to structural size) was estimated by calculating *Z*-standardized residuals of the linear regression of body mass on wing length and changes in body mass and body condition by differences between final and initial values. Data are expressed as means ± SE; the differences were tested by *t* tests.

portion of males in the brood was analyzed by logistic regression with binomial errors and logit links. To avoid pseudoreplication, I considered each nest ($n = 30$) as the unit for statistical analysis. The dependent variable in the analysis was the number of males in the brood, and the binomial denominator was the brood size (number of nestlings sexed). The degree of discrepancy between the model and the data is given by deviance, which is asymptotically distributed as chi-square (Crawley, 1993). Deviations from the binomial model were tested using the deviance of the null model. Correlation coefficients were calculated by $r = \text{SSXY}/(\text{square root SSX} \cdot \text{SST})$, where SSXY stands for the sum of the products $\times$ y, SSX is the sum of squares for x, and SST is the total sum of the squares (Crawley, 1993). All tests were two-tailed and the α level was set at 5%.

RESULTS

Experimental effects on adult condition

In the handicapped females one nest was deserted by the parents, and in the control group one female was not recaptured. In total, 18 out of 20 females were recaptured at end of the experiment when the chicks were 45–50 days old. The manipulation of flight costs produced significant differences in body mass and body condition between the experiment birds and controls (Table 1). The index of feather growth was higher in the control group, but the difference was not significant (Table 1). Neither the brood sex ratio nor the interaction with treatment had any significant effect on female mass (sex ratio: $F_{2,18} = 0.21$, $p = .81$; sex ratio * treatment: $F_{1,18} = 0.001$, $p = .97$), female body condition (sex ratio: $F_{2,18} = 1.10$, $p = .37$, sex ratio * treatment: $F_{1,18} = 0.98$, $p = .34$) or feather growth index (sex ratio: $F_{2,18} = 0.81$, $p = .47$, sex ratio * treatment: $F_{1,18} = 1.68$, $p = .22$). The change in body condition in handicapped females did not correlate with body condition before treatment (Spearman rank correlation, $r_{s9} = .32$, $p = .40$). Moreover, the body condition change of handicapped females was independent of the number of males reared (Kruskal-Wallis test, $\chi^2_9 = 0.839$, $p = .66$).

Table 2

Number of blue-footed booby clutches with different sex combinations in control and handicapped groups

	Brood sex ratio		
	Two males	Male and female	Two females
Handicapped ($n = 9$)	2	6	1
Control ($n = 10$)	3	6	1

Differential effects on sons and daughters

There was no chick mortality in the chicks marked at hatching except in the nest deserted by the parents. There were no differences in brood sex combination between the control and experimental groups (Table 2; $G = 0.15$, $p = .93$). The offspring sex was not related to hatch order ($G = 0.99$, $p = .61$). The handicapping of females had a significant effect on chick mass, with daughters in the handicapped group approximately 8% lighter (mean = 135 g) than those in the control group (Figure 1 and Table 3). However, the mass of the sons was similar in both groups (Figure 1). Thus, the interaction between the sex of the chicks and the experiment was significant (Table 3). Hatch order had a significant effect on chick mass; the first-hatched chicks were heavier (Table 3). Interactions between sex and hatch order and between hatch order and treatment were not significant (Table 3).

The sex of the chicks had no effect on nestling wing length as measured at 45 days of age (Table 3 and Figure 1). Even the experiment had no effect on nestling wing length; the effect of the interaction between the sex of the chick and the experimental group was significant (Table 3). Female nestlings in the handicapped group had shorter wings than females in the control group, although this did not occur in male nestlings (Figure 1). No significant difference in wing length was found between chicks hatched at different order (Table 3). Moreover, neither interactions between hatch order and sex, nor between hatch order and experimental group, were significant (Table 3).

Adult condition and sex ratio

All chicks were sexed before the experiment. The proportion of sons in two-chick broods ($n = 30$) decreased with female mass ($r = -.33$, $p = .039$) and with female body condition ($r = -.41$, $p = .011$) at hatching (when the chicks were less than 7 days old). Thus, the brood sex ratio of females in poorer conditions was male biased, and the brood sex ratio of females in better conditions was female biased (Figure 2).

DISCUSSION

Reduced maternal effort differentially affects sons and daughters

I found that reduced maternal effort affected daughters more than sons in two-chick broods. Female chicks in the experi-

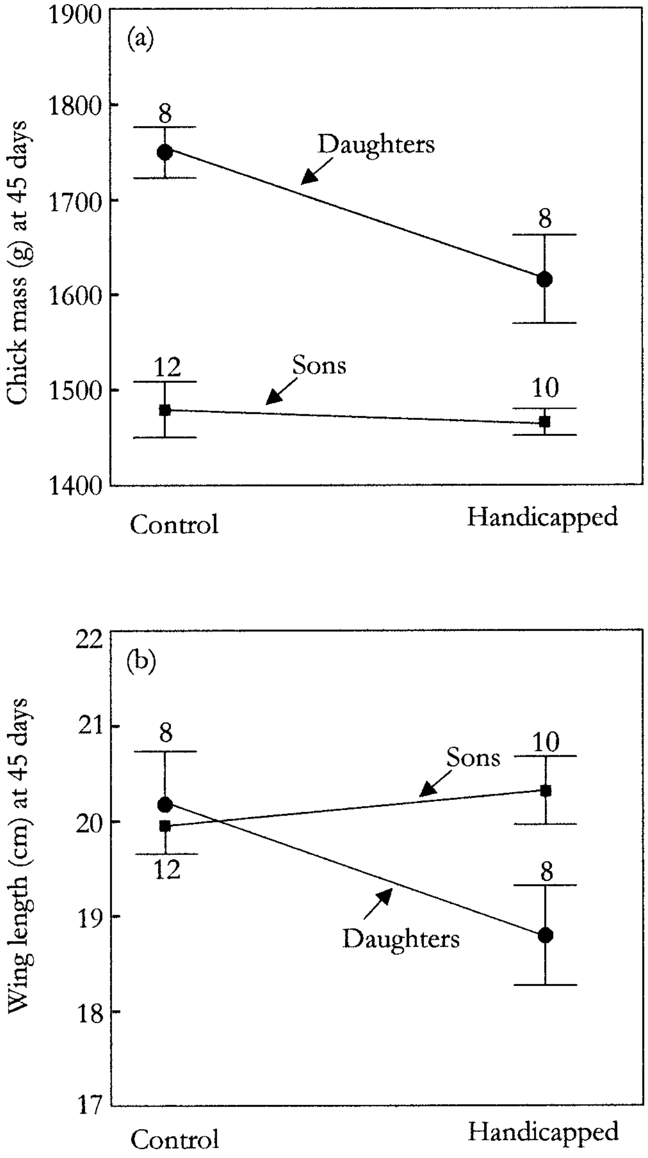

Figure 1
Mean (± SE) of (a) mass and (b) wing length of blue-footed booby male (squares) and female (circles) nestlings in the handicapped and control groups at 45 days old. The numbers denote sample size.

mental group had lower mass and shorter wing lengths than the controls. However, this effect was not found in male chicks. Moreover, handicapped females reduced their body condition independently of the number of daughters reared.

These results support the hypothesis that female chicks are more affected by maternal condition than are male chicks. This differential effect on daughters could be because female chicks are larger and grow faster than male chicks (Drummond et al., 1991). My results agree with other studies that show that female booby chicks are more vulnerable to food-related stress than male chicks. Thus, on Isla Isabel, Mexico, female chick mortality, but not male chick mortality, increased with the hatching sequence in later broods (Torres and Drummond, 1997). The greater vulnerability of female chicks to starvation could be due to their faster growth rates, their higher energetic costs, sex-biased parental care under food stress, or a combination of all three factors.

Table 3

Three-way ANOVAs of the effect of the experimental group (i.e., membership of the control or handicapped group), the sex of the chick, and the position at hatching on body mass and wing length in booby chicks at 45 days of age (see Figure 1)

	Body mass			Wing length		
Source	df	*F*	*p*	df	*F*	*p*
Group	1	6.70	.015	1	1.51	.23
Sex	1	56.20	<.001	1	1.34	.25
Hatch order	1	4.20	.049	1	2.30	.14
Group * sex	1	5.33	.025	1	4.45	.043
Group * hatch order	1	1.81	.19	1	0.14	.71
Sex * hatch order	1	0.28	.59	1	0.64	.43
Error	31			31		

In this species, there is no evidence that daughters require a greater parental investment than sons, but in a field experiment, Torres and Drummond (1999a) showed that female chicks had higher growth rates than male chicks when hand-fed the same amount of food. This suggests that there may be different strategies of resource allocation for the two sexes of chicks. One possibility is that males could have accelerated neuromotor development, whereas females grow faster (Teather and Weatherhead, 1994; Torres and Drummond, 1999a). Different resource allocation for the sexes could explain the difference in responses to starvation. Under food stress, males are able to develop their locomotor requirements slowly, but females grow slowly and increase their risk of mortality (Torres and Drummond, 1999b). Moreover, although females grow faster with the same amount of food, over the whole growth period they may be more expensive to rear.

Another explanation for a sex-specific response to parental

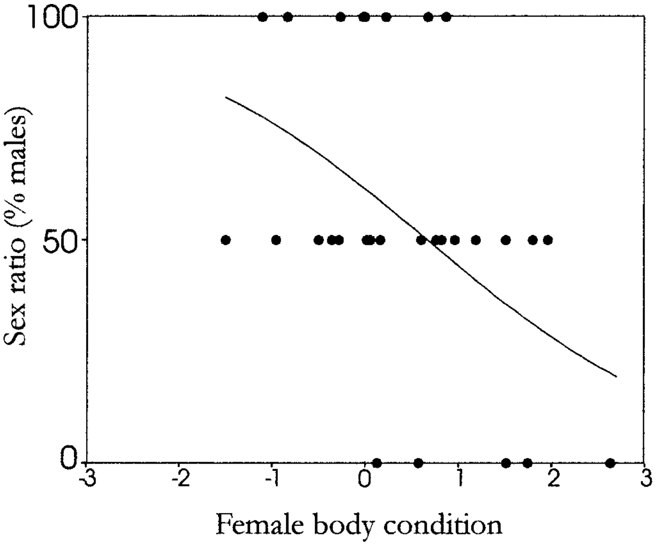

Figure 2
Proportion of sons in relation to female body condition at hatching (when the chicks were less than 7 days old) in blue-footed boobies on Isla de Lobos de Tierra (n = 30 broods). The female body condition was estimated by calculating the residuals of the linear regression between body mass and wing length. The residuals obtained were standardized in a Z normal distribution. High values of body condition indicate females in good condition and low values indicate females in poor condition. Analyses were performed using logistic regression. An adjusted curve is shown: proportion of sons = exp[0.47–0.70(female body condition)]/1 + exp[0.47–0.70(female body condition)]; $F_{1,29}$ = 7.41, p = .011.

manipulation could be sex-biased parental care (Stamps, 1990). Parents could invest less in female offspring when resources are scarce. Such a biased investment would be expected if the payoff in increased body reserves at the time of independence is different for the two sexes under these conditions. Nevertheless, there is little evidence for sex-biased investment in birds (Leonard et al., 1994; Lessells et al., 1998; Stamps, 1990).

Sex ratio

The results of my study demonstrate that maternal condition affects the mass and size of female more than male offspring. Seabird species exhibit positive correlations between mass at fledging and subsequent survival and lifetime reproductive success (Jarvis, 1974; Perrins et al., 1972; Spear and Nur, 1994; but see Harris and Rothery, 1985; Velando, 2000). Consequently, female boobies can suffer a fitness disadvantage if their mothers are in poor condition. This difference in fitness between the sexes can be a selective force for sex ratio manipulation.

Numerous studies have shown that female birds adjust their clutch size, egg size, and egg constituents at the time of egg laying in accordance with their current body condition (e.g., Ankney and MacInnes, 1978; Bolton et al., 1992; Boutin, 1990; Martin, 1987; Nager and van Noordwijk, 1992). Females can also adjust the sex ratio of their broods in accordance with the potential fitness gain for each sex in relation to their body condition (Charnov, 1982; Frank, 1990; Trivers and Willard, 1973). Females that do so should be fitter than those lacking such ability if the fitness benefits of biased sex ratios are greater than the cost of changing the allocation between sons and daughters. Establishing the mechanism by which sex ratios are adjusted remains a major challenge, and in vertebrates it has been suggested that birds are constrained in their abilities to change sex determination (Williams, 1979). However, recent studies suggest that birds may not be as constrained as previously once thought (see Oddie, 1998).

In blue-footed boobies there is some correlative evidence that females can adjust the sex ratio of their offspring in response to their condition, suggesting a maternal control on egg sex ratio or, alternatively, that daughters have higher mortality rates (Torres and Drummond, 1997). On Isla Isabel, fledgling sex ratios were related to food supply; when food was scarce and presumably females were in poor condition, the sex ratio was male biased (Torres and Drummond, 1999b). Moreover, in these years, the fledging sex ratio varied seasonally, probably in response to a variation in food availability during the season (Torres and Drummond, 1999b). On Isla Lobos de Tierra, all chicks were sexed, and the hatching sex ratios were related to female body condition (Figure 2). Overall, these results suggest that sex ratio variation in blue-footed boobies is an adaptive response to the feeding condition of females.

Life history and the regulation of parental effort

I found that female blue-footed boobies with experimentally increased flight costs showed a decrease in their own condition and in that of their chicks. Thus, the first prediction of this study was not fulfilled. This prediction was based on the fixed investment hypothesis that parental effort in long-lived seabirds is restricted to a fixed level of investment in the current offspring in order to maximize adult survival (Sæther et al., 1993). This hypothesis has been supported by handicapping experiments at the chick stage in Procelliiformes, which found that handicapped adults did not vary their condition after manipulation but transferred the cost of the handicap to the condition of their chicks (Mauck and Grubb, 1995; Sæther et al., 1993; Weimerskirch et al., 1999; but see Weimerskirch et al., 1995). However, I found that adult female boobies with increased flight cost used up their own reserves. The different conclusions between these studies could be due to a difference in the experimental manipulation. I increased the cost of flight by approximately 5%, while the Procellariforme studies increased cost of flight by approximately 9–10%. The amount by which flight costs were increased in this study is unlikely to have compromised future survival. Adult seabirds can have a small buffer of nutritional reserves that can be used in the current reproduction without compromising their future survival. However, even a small reduction in body mass at the end of reproduction may have dramatic effects on adult survival. In the kittiwake (*Rissa tridactyla*), Jacobsen et al. (1995) found that a reduction of 5% in adult body mass at the end of reproduction, similar to my study, decreased the probability of adult survival by 23%. Thus, other studies that have manipulated the cost of reproduction by increasing chick requirements have shown that seabirds have a flexible investment in their young (Erikstad et al., 1997; Jacobsen et al., 1995; Johnsen et al., 1994; Reid, 1987).

My results best fit the flexible investment hypothesis (Johnsen et al., 1994). Female boobies may adjust their own resources in order to maximize their lifetime reproductive success in a stochastic environment (Erikstad et al., 1997). Seabirds live in variable environments with large annual fluctuations in breeding conditions; the fitness value of their offspring can depend on breeding conditions. Under poor conditions the offspring produced have a lower fitness value than those produced in good breeding conditions, when there is a higher chance of survival (Erikstad et al., 1998).

Environmental conditions in the Humboldt upwelling system off the Peruvian coast change dramatically with the occurrence of El Niño (Glynn, 1990), and there are great repercussions on the population size and reproductive performance of seabirds (e.g., Jahncke, 1998; Ribic et al., 1992). In 1998–1999, the boobies on Isla Lobos de Tierra had a good breeding season with low chick mortality (no chicks died during my study) and abundant anchovies, corresponding to the cold-rich phase after El Niño 1997–1998 (Goya E, personal communication). Thus, offspring raised in these conditions would have a better chance of survival. Adult boobies might be selected to risk some of their future survival to produce young in good years. Similar experimental studies on blue-footed boobies in poorer environmental conditions are needed to understand how this species optimizes its lifetime reproductive success.

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