Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby

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Summary

1. In long-lived species, such as seabirds, the allocation of resources between self-maintenance and reproduction is of particular interest because only a small reduction in adult survival may have a large negative effect on lifetime reproductive success. There is much debate about whether seabirds have a fixed or flexible level of investment in their current reproduction, and it has been proposed that parents can regulate the risk of an increase in mortality under the control of a mass threshold.

2. Body mass change as response to experimental manipulations of parental effort was examined in blue-footed boobies (*Sula nebouxii* Mine-Edwards), a sexually size-dimorphic seabird, with females approximately 31% heavier than males.

3. First, paternal effort was manipulated by trimming the flight feathers and thereby handicapping males during the chick-rearing period. Mass remained stable in handicapped males, while there was a reduction of female body mass as response to the handicapped partner. The handicapping of males had a significant effect on chick mass.

4. Secondly, an experiment was made by enlarging and decreasing broods of two chicks to three and one during the first week after hatching. Body mass of females, but not males, was lower in enlarged broods, and body mass of males, but not females, was higher in the reduced broods when the chicks were 45 days old. Chick body masses were lower among enlarged broods than among reduced and control broods.

5. Overall, these and other results revealed that blue-footed boobies have a sex-specific body mass regulation. Males had a fixed body mass at the end of experiments; they were working at some physiological maximum or were unwilling to pay the cost in terms of future survival, when the effort demanded was increased. Females performed a flexible effort and were working with a buffer of nutritional reserves that they used when necessary. Below a critical level, females preferentially allocated resources to the maintenance of their body condition at the expense of investment in current reproduction.

Key-words: body mass threshold, brood size manipulation, handicapped males, sex-related breeding effort, *Sula nebouxii*.

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Introduction

Trivers (1972) defined parental investment as 'any investment by the parent in an individual offspring that increases the offspring chances of surviving at the cost of the parent ability to invest in other offspring'. A central

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point in life history theory is that parental investment in current reproduction should be balanced by the costs in terms of residual reproductive value (Williams 1966; Stearns 1992). For many bird species, the nestling rearing phase is a critical period for decisions influencing this balance (Drent & Daan 1980). During this period, breeding birds must decide how to allocate the energy they gather between themselves and their offspring. In short-lived passerines, the probability of survival to future reproduction is low, so an increase of parental effort at the expense of their survival would be

expected in response to an increment in chick demand (Linden & Møller 1989). In contrast, in long-lived species such as seabirds current reproductive investment is more likely to be regulated by the impact of reproductive effort on the future reproduction of the parents, and the adults should be restrictive in increasing effort (Drent & Daan 1980; Linden & Møller 1989). Nevertheless, in seabirds, the studies of experimentally increased reproductive effort have shown differing results, with costs of reproduction passed to offspring (intergenerational costs; Harris 1966; Jarvis 1974; Ricklefs 1987; Sæther, Andersen & Pedersen 1993; Mauck & Grubb 1995), absorbed by parents (intragenerational costs; Reid 1987; Weimerskirch, Chastel & Ackermann 1995), or shared (Jacobsen, Erikstad & Sæther 1995; Tveraa, Lorentsen & Sæther 1997; Weimerskirch, Prince & Zimmermann 2000).

There is much debate about how seabirds optimize the balance between current reproductive effort and future reproduction, and two main mechanisms have been proposed. The 'fixed investment hypothesis' posits that seabirds have a fixed level of investment in their current reproduction, independently of offspring requirements (Ricklefs 1987; Sæther, Andresen & Pedersen 1993; Mauck & Grubb 1995). The 'flexible investment hypothesis' suggests that long-lived birds have a flexible reproductive effort according with offspring demand and condition (Reid 1987; Johnsen, Erikstad & Sæther 1994; Jacobsen *et al*. 1995; Weimerskirch *et al*. 1997). These two mechanisms are not mutually exclusive, and energy allocation during reproduction should be dependent upon breeding condition: when food is easily available and parents are in good condition they can compensate to some extent to chick requirements, but they may be unable to do so when resources are less available (Erikstad *et al*. 1997; Erikstad *et al*. 1998; Weimerskirch *et al*. 2000; Weimerskirch, Zimmermann & Prince 2001). In this context, permanent monitoring of own body condition should be essential in reproductive decisions (Drent & Daan 1980), and parents could regulate the risk of an increase in mortality under the control of a mass threshold (Monaghan, Uttley & Burns 1992; Chaurand & Weimerskirch 1994; Olsson 1997). In fact, evidence is accumulating that adult body mass plays an important role in foraging behaviour, food provisioning and regulation of parental effort in seabirds (Monaghan *et al*. 1989; Chaurand & Weimerskirch 1994; Chastel, Weimerskirch & Jouventin 1995; Erikstad *et al*. 1997; Tveraa *et al*. 1997; Dearborn 2001; but see Wernham & Bryant 1998).

In addition to their body condition and food availability, females should optimize their breeding decisions in relation to the level of effort of the partner (Chase 1980; Houston & Davies 1985; Winkler 1987). In species with biparental care, a conflict between sexes over division of work probably occurs (Trivers 1972). The reduction of feeding effort by one partner should, in most cases, result in an increased effort by the other (Winkler 1987), as was supported by several studies in short-lived passerines (e.g. Wright & Cuthill 1989, 1990; Whittingham, Dunn & Robertson 1994; Markman, Yom-Tov & Wright 1995; Sanz, Kranenbarg & Tinbergen 2000). As far as we know, only two studies have tested the compensatory response in long-lived birds, showing that a decrease in the incubation effort by one partner produces a compensatory response by the other partner depending on its body condition (Tveraa *et al*. 1997; Dearborn 2001).

The best way to explore the relationship between current reproductive effort and the cost imposed on future reproduction may be by experimental manipulations of reproductive effort (Reznick 1985; Partridge & Harvey 1988). As a model, experimental modifications of brood size in birds have been studied (Linden & Møller 1989; Dijkstra *et al*. 1990; Stearns 1992). Despite a large number of brood size experiments to study the cost of reproduction in short-lived birds (Dijkstra *et al*. 1990; Murphy 2000), few have involved long-lived birds and results have been mixed (e.g. Golet, Irons & Estes 1998). Manipulation of brood size does not manipulate the reproductive effort directly (Lessells 1991; Lessells 1993), and assumes reproductive costs representing a linear function of brood size. However, some general models predict that the optimal response could yield a decrease, no response or even an increase in effort with increasing brood size (Winkler 1987; Tammaru & Hörak 1999). Brood size enlargements might have limited ability to detect reproductive costs, because the parents may reduce their parental effort adaptively (Tammaru & Hörak 1999). Thus, results of brood size manipulations should be compared with other studies that manipulate parental effort, such as handicap experiments, to understand better the breeding decisions involved.

The blue-footed booby (*Sula nebouxii* Mine-Edwards) is a potentially interesting species for examining sexual differences in the regulation of parental body condition during the breeding season. In this long-lived species (annual survival rate > 90%; Croxall & Rothery 1991), females are approximately 31% heavier than males during the breeding season (Nelson 1978) and recruit at an earlier age (Osorio-Beristain & Drummond 1993). In contrast with many seabirds with similar parental roles, female boobies feed chicks three times more than do males (Anderson & Ricklefs 1992; Guerra & Drummond 1995). Males forage inshore, close to the colony, and females make longer trips to offshore waters (Nelson 1978). In a recent study, female boobies with experimentally increased reproductive effort (shortened wing span) reduced their body condition and shared the cost with their offspring (Velando 2002). In addition to that experimental study, here we reported two experiments: the manipulation of the amount of effort by the male and a brood size manipulation. The main objective of this study was to investigate body condition regulation by examining: (1) how females respond to reduced effort by their partners; (2) whether males and females have a flexible or fixed body condition regulation in response to reproductive effort manipulation; and (3) whether

parental effort is regulated by a body mass threshold comparing the adult body mass in three different experimental studies that increased reproductive effort in the same season.

Materials and methods

STUDY AREA AND ENVIRONMENTAL CONDITIONS

This study was conducted on the island Lobos de Tierra (06°28′ S, 80°50′ W) located near the Peruvian coast during the summer of November 1998 to January 1999. More than 10 000 pairs of blue-footed boobies breed on the plains or on the slopes and in flat valleys, possibly the world's largest colony of the species (Nelson 1978). In one large aggregation, numbered stones were used to mark nests with one or two eggs. In Lobos de Tierra, chicks hatched from December to March (A. Velando, unpublished data); the first chick in each nest hatched between 1 and 17 December, so the selected nests were early. In order to avoid nest desertion by adults (see below), earlier nests were assigned to handicapping experiments. Thus, 30 two-egg nests were selected to be used in another study that included the handicap manipulation of adult females; chicks hatched between 1 and 12 December (see Velando 2002). The remaining nests were used in two different experiments for the present study. The sequential allocation of experiments introduced a slightly seasonal bias (5 days) that should be taken into account in between experiment comparisons (see Data analysis).

In Isla Lobos de Tierra the overall reproductive success was high in the 1998–99 season. Thus, only 12 of 274 chicks monitored died from starvation. Chick losses slightly increased with season, from no mortality in the first week of study (female handicap experiment: Velando 2002) to 7% in the latter study (brood size manipulation). When food is scarce during the nestling period, brood reduction is common in this species (Drummond & García Chavelas 1989). Environmental conditions in the Humboldt upwelling system off the Peruvian coast change dramatically with the occurrence of El Niño (Glynn 1989), with great impact on the population size and reproductive performance of seabirds (e.g. Ribic, Ainley & Spear 1992). During the 1998–99 season the boobies on Isla Lobos de Tierra had a good breeding season with low chick mortality and abundant anchovies, corresponding to the cold–rich phase after El Niño 1997–98 (Jahncke & Goya 2000; E. Goya, personal communication). Thus, we assumed that our experiments were made under conditions of food abundance.

MANIPULATION OF MALE FLIGHT COST

Twenty-two marked nests with two hatchlings were used for this experiment. The chicks in each nest hatched between 6 and 12 December. Nests were assigned by random choice to two treatment groups. We captured the male parents on the marked nests when the senior chick was less than 7 days old. Adult boobies were captured early in the morning to avoid heat stress. In the 11 experimental nests the adult males were handicapped and in the 11 control nests the adult males were captured and handled but not handicapped. The handling time was similar for both groups of birds. The captured adults were ringed, measured and weighed. There was no nest desertion in either group during the experiment.

Ethical considerations were taken into account in the experimental design in order to minimize the damage caused by increasing flight costs whil 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 the damage is permanent when the individual is not recaptured. A handicap produced by clipping feathers and thereby reducing wing span will disappear soon after the normal post-breeding moult and will have a less dramatic effect on flight performance (Cuthill 1991; Mauck & Grubb 1995).

Previous handicap studies on seabirds increased the cost of flight by 9–10% (e.g. Sæther *et al*. 1993; Mauck & Grubb 1995; Weimerskirch, Fradet & Cherel 1999), and in some of these studies also caused nest desertion by some adults (Sæther *et al*. 1993; Weimerskirch *et al*. 1999). Thus, a proportion of handicapped adults will be expected to desert when a similar increase is used. To avoid this and keep the number of subjects needed as low as possible, increasing the flight cost by approximately 5% was decided. Each primary remige was cut 2·5 cm shorter, measuring from the tip and perpendicularly to the long axis. Reducing the male wing span by 5 cm (the average mass for a male is 1473 g of mass and the average wing span is 149 cm) increased the cost of flight by approximately 5% (see Pennycuick 1989 for calculations).

BROOD SIZE MANIPULATION

The clutch size of the blue-footed booby varied from one to three eggs, although more than 80% of the nests contained only two eggs (A. Velando, unpublished data). In the brood experiment, 75 marked nests with two hatchlings were used. Broods at 25 nests were enlarged from two to three chicks (enlarged treatment), 25 broods were reduced from two to one chick (reduced treatment) and 25 nests were assigned as control. Brood sizes were manipulated during the first week after hatching. The size of the adopted chicks was always intermediate between the sizes of new siblings. This was undertaken to minimize the effect of dominance among siblings (Drummond & Osorno 1992). There is no parent–offspring recognition during the first week after hatching in Sulidae, and parents accept any chick they find in their nests (Nelson 1966; Jarvis 1974). Chicks in the

control treatment were handled as much as the chicks in reduced and enlarged broods. The handling time was similar among treatments. The chicks in each nest used in the brood size experiment hatched between 10 and 17 December. The sample size was reduced due to the loss of one control nest. Additionally, in order to compare with parents with different initial brood size, 20 unmanipulated broods with one hatchling from one-egg nests were included (group of one-chick broods).

CHICK GROWTH AND ADULT BODY MASS

In the flight cost and brood size experiments, chicks were marked individually according to hatching sequence with indelible coloured markers on their bills. At around 10 days old, each chick was tagged with a strip of velcro on its tarsus bearing a unique number. At 45 days of age, each chick was captured (broodmates were captured on different days due their age difference); it was then weighed with a spring balance, its wing length was measured using the wing chord flattened method with a metallic ruler with a stop and its tarsus, culmen and bill length were measured with a calliper. The morphometric measurements of chicks allowed sexing by means of a discriminant analysis. The discriminant function was obtained from data of 70 chicks (including those from the female handicap experiment) measured at 45 days of age and sexed by molecular analysis (Velando 2002). This discriminant function classified 97% of the chicks (discriminant function: $-45 \cdot 56 + 0 \cdot 58$ tarsus $+ 0 \cdot 14$ wing, Wilks' lambda $= 0 \cdot 22$, $P < 0 \cdot 001$) correctly. Adults were sexed by voice and eye examination (Nelson 1978).

Adults were captured, measured (except males in handicap experiment) and weighed with a spring balance when the senior chicks were 45–50 days old. Due to the difficulties in capture and manipulation of adults, we prioritized capturing both adults in most pairs of the handicap experiment, and one adult per nest in the brood size experiment. Sampling just one adult for nest meant that we could not investigate the different effects of brood size manipulations in both members of pairs simultaneously. In the latter experiment, we concentrated on adults of broods that maintained their manipulated or control size at the end of the experiment.

DATA ANALYSIS

In both sexes adult body size, measured as wing length, did not correlate with adult body mass when the senior chicks were 45–50 days old ($P > 0 \cdot 1$). Nevertheless, in order to control for any possible effect of structural body size on adult body mass variation at the individual level, we performed analyses of covariance (ANCOVA). Thus, body mass was compared among groups after removing the effect of body size, which was measured as wing length and introduced as covariate; the analysis of condition by ANCOVA has been recommended repeatedly (García-Berthou 2001; Hayes & Shonkwiler 2001).

In the male handicap experiment, the adult body mass of males and females when the chicks were 45–50 days old were analysed independently compared because the males were manipulated at the beginning of the experiment (two repeated measures), and the females were captured only at the end of the experiment. Thus, we performed a two-way ANCOVA in each sex on the final body mass with treatment (control and male handicapped groups) as factor and wing length as covariate. In the brood size experiment, adult body mass at the end of the experiment was analysed using a two-way ANCOVA of the effect of treatment (control, enlarged or reduced brood) and sex on body mass controlled by wing length as covariate. Body mass differences between groups were compared by *post-hoc* analyses (LSD). In addition, adult body mass in the group of one-chick broods was compared with the adult body mass in the control and reduced groups by *t*-tests.

The adult body mass in the three experiments where an increase in reproductive effort was induced in the same season (including the female handicap experiment: Velando 2002) was analysed using an ANCOVA with experiment (female handicap, male handicap and brood size manipulation), treatment (control and experimental increased effort groups) and sex as factors and hatching date and wing length as covariates. Then, body mass was compared between groups by LSD *post-hoc* analysis. In the blue-footed booby, female chicks may be more expensive to rear (Velando 2002), and a greater number of female chicks reared may impose an extra cost. Thus, the relationship between the number of females reared and adult body mass was analysed by Kendall's rank correlation. Moreover, the sex was included in the chick mass analyses because reduced parental care would affect daughters more than sons (Velando 2002).

In the male handicap experiment, the effects of experiment, sex and hatch order on chick mass at 45 days were studied by analysis of variance (ANOVA). The brood sex ratio was similar between experimental and control groups (54 and 55% of males, respectively; $P > 0 \cdot 5$). In the brood size experiment, within-nest average mass was computed separately for male and female chicks, thus accounting for different brood size due to experimental manipulations and for sexual dimorphism. According to the analysis of adult birds (above), chick mass at 45 days of age was compared among experimental groups (i.e. enlarged, reduced and control groups). The differences between groups were tested with LSD *post-hoc* analyses on the main effects. In addition, chick mass in one-chick broods was compared with chick mass in the control and reduced groups by *t*-tests. There was chick mortality in the four groups (see Results). To standardize the effect of brood manipulations, only broods that maintained their manipulated or control size at the end of the experiment were used in the analyses. Similar results are achieved whether broods that suffered mortality are included in the analysis. All tests were two-tailed and the alpha level was set at 5%.

Results

MANIPULATION OF MALE FLIGHT COST

One chick died in the experimental group, and none in the control group. A three-way ANOVA of the effects of treatment, sex and hatch order on chick mass was performed. Female chicks were heavier than male chicks (Fig. 1; sex: $F_{1,35} = 40.50$, $P < 0.001$). The handicapping of males had a significant effect on chick mass (Fig. 1; experimental group: $F_{1,35} = 5.24$, $P = 0.028$). The interaction between the sex of the chicks and treatment was non-significant ($F_{1,35} = 2.63$, $P = 0.11$; power = 0.34). Hatch order and interactions between sex and hatch order and between hatch order and treatment were not significant (hatch order: $F_{1,35} = 2.63$, $P = 0.38$; sex × hatch order $F_{1,35} = 1.60$, $P = 0.21$; group × hatch order: $F_{1,35} = 0.04$, $P = 0.84$).

The manipulation of flight costs in the adult males did not produce significant differences in body mass and body mass changes between both experiment groups (Table 1). Nevertheless, there was a significant effect of the handicap on their partners. At the end of the experiment, females paired with handicapped males were 5% lighter than those paired with control males (Table 1). The final body mass of handicapped males or their

partners was independent of the number of female chicks reared (Kendall's rank correlation; handicapped males: $\pi = 0.41$, $P = 0.13$; female partners of handicapped males: $\pi = 0.26$, $P = 0.40$).

BROOD SIZE MANIPULATION

Only seven of 94 nests lost one or more chicks (8% in enlarged, 8% in reduced and 8% in control II and 5% in one-chick broods). The number of 45-day-old chicks raised per pair differed significantly between groups (Kruskal–Wallis test; = 83.18, $P < 0.001$). Thus, pairs with enlarged broods raised more chicks (mean ± SE: 2.92 ± 0.07, number of clutches $n = 25$) than control broods (1.86 ± 0.13, $n = 24$) and control raised more chicks than reduced (0.95 ± 0.05, $n = 25$) and one-chick broods (0.95 ± 0.04, $n = 20$).

A two-way ANOVA of the effect of experimental group (control, enlarged or reduced brood) and sex on chick body mass showed that female chicks were heavier than male chicks (Fig. 2; sex: $F_{1,83} = 197.87$, $P < 0.001$) and that treatment had a significant effect on chick mass (Fig. 2; experimental group: $F_{2,83} = 7.17$, $P = 0.001$). The interaction between sex and experimental group was not statistically significant ($F_{2,83} = 2.29$, $P = 0.10$; power = 0.47). Chicks in the enlarged broods were lighter than
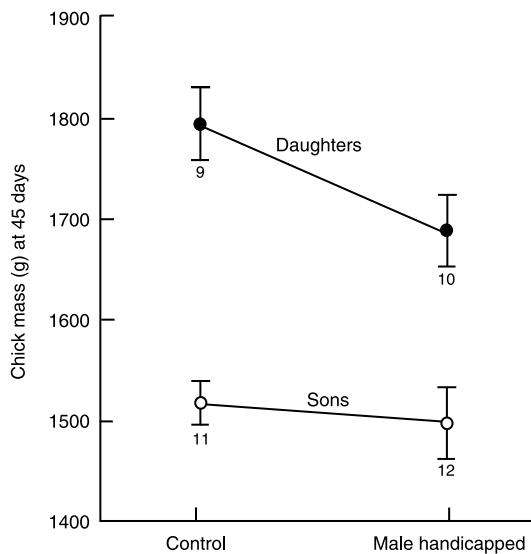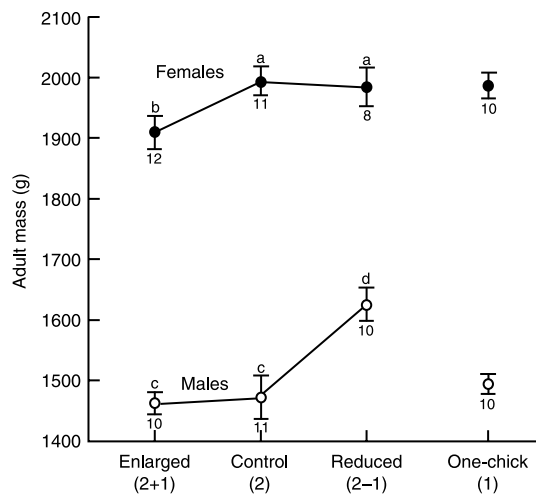

Fig. 1. Mean (± SE) of mass of blue-footed booby male (○) and female (●) nestlings in the male handicapped and control groups at 45 days old. The numbers denote sample size.
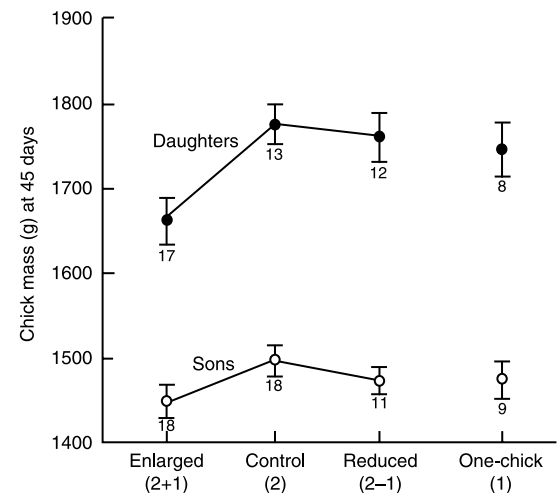
Fig. 2. Mean (± SE) of mass of blue-footed booby male (○) and female (●) nestlings in the experimental enlarged, reduced and control broods (original two-egg clutches) and unmanipulated one-chick broods at 45 days old. The line indicates the experimental groups and the numbers denote sample size.

Table 1. Differences in condition and body mass of adult blue-footed boobies captured at the end of the experiment, when the chicks were 45–50 days old, between control and male handicapped groups. Body mass changes are the final minus initial values. The differences between groups were tested by ANCOVAs of the effect of the experimental group on body mass controlled by wing length as covariate. Data are expressed as mean ± SE, sample sizes are given between parentheses
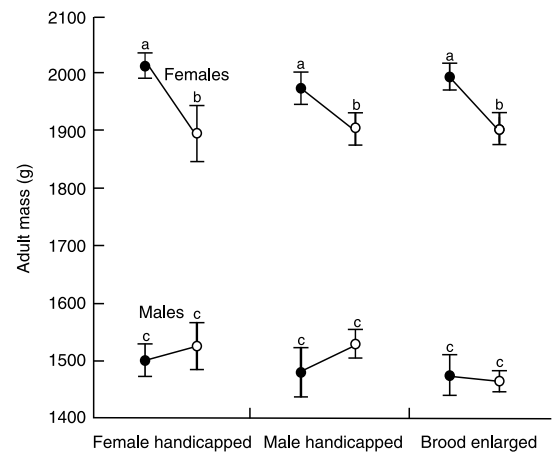
Variable	Control	Male Handicapped	F	P	Power
Male body mass (g)	1477 ± 42 ($n = 9$)	1554 ± 26 ($n = 11$)	2.55	0.13	0.34
Male body mass change (g)	74.56 ± 43.81 ($n = 9$)	12.27 ± 32.30 ($n = 11$)	1.26	0.28	0.20
Female body mass (g)	1987 ± 28 ($n = 11$)	1897 ± 25 ($n = 10$)	5.89	0.02	0.63

Fig. 3. Mean (± SE) of mass of blue-footed booby male (○) and female (●) adults captured at the end of the experiment, when the chicks were 45–50 days old, in the experimental enlarged, reduced and control broods (original two-egg clutches) and unmanipulated one-chick broods. Line indicates the experimental groups and the numbers denote sample size. Results of LSD pairwise comparisons from a two-way ANCOVA are showed; different letters means significant differences ($P < 0.05$).

Fig. 4. Summarized results of stressful experiments on body mass (mean ± SE) of blue-footed booby male and female adults captured at the end of the experiment, when the chicks were 45–50 days. The lines connect control (○) with experimental groups (●). Results of LSD pairwise comparisons are showed: different letters means significant differences ($P < 0.05$).

those in the control and reduced groups (Fig. 2; LSD tests; enlarged vs. control: $P = 0.003$; enlarged vs. reduced: $P = 0.027$), and the mass of chicks in reduced and control groups did not differ (Fig. 2; LSD test: $P > 0.5$). Chicks in the one-chick broods had similar body mass than control chicks (Fig. 2; females: $t = 0.81$, $P = 0.43$; males: $t = 1.04$, $P = 0.30$) and chicks in the reduced broods (Fig. 2; females: $t = 0.34$, $P = 0.73$; males: $t = 1.01$, $P = 0.32$).

In total 62 adults were captured at end of the experiment, when the chicks were 45–50 days old. A two-way ANCOVA of the effect of experimental group (i.e. parent of the control, enlarged or reduced brood) and adult sex on body mass controlled by wing length as covariate showed a significant effect of treatment and sex on parent body mass (Fig. 3; experimental group: $F_{2,55} = 8.35$, $P = 0.001$; sex: $F_{1,55} = 111.44$, $P < 0.001$). The interaction between the sex of the parent and the experiment group was also significant (see Fig. 3; $F_{2,55} = 4.19$, $P = 0.020$). Females were heavier than males. Females rearing enlarged broods had lower body mass than those rearing control and reduced broods, both of which had similar body mass (Fig. 3). Meanwhile, males showed a different pattern. The males rearing enlarged broods had similar body mass to those rearing control broods, but in both groups the males lost more mass during the fledgling period than males with reduced broods (Fig. 3). In the enlarged group, the body mass of male and female adults was independent of the number of females reared (Kendall's rank correlation; males: $\pi = -0.10$, $P = 0.73$; females: $\pi = -0.21$, $P = 0.41$). Males and females rearing unmanipulated broods with one chick had similar body mass to control parents rearing two chicks (Fig. 3; females: $t = 0.21$, $P = 0.84$; males: $t = 0.79$,

$P = 0.44$). Males, but not females, rearing unmanipulated broods with one chick had lower body mass than males rearing one chick in reduced broods (Fig. 3; females: $t = 0.09$, $P = 0.92$; males: $t = 4.06$, $P = 0.001$).

COMPARISON OF INCREASED REPRODUCTIVE EFFORT EXPERIMENTS

In the same season, we conducted a handicap experiment on adult females (Velando 2002). The effects on adult body mass are summarized in Fig. 4 and compared with the results reported above. The effect of increased effort on body condition was similar in the three experiments (Fig. 4; experiment: $F_{2,102} = 0.75$, $P = 0.47$), and interactions between experiment and treatment and between experiment and sex were not significant (experiment × treatment $F_{2,102} = 0.75$, $P = 0.47$; experiment × sex: $F_{2,102} = 1.13$, $P = 0.33$). There was no effect of the season nor of the interaction between season and treatment on body condition (hatching date $F_{1,102} = 0.08$, $P = 0.77$; treatment × hatching date: $F_{1,102} = 0.21$, $P = 0.65$). In fact, the body mass of adults did not correlate with hatching date in either the control or the increased effort groups: (Pearson product–moment; control: males, $r_{31} = 0.24$, $P = 0.20$; females, $r_{32} = -0.15$, $P = 0.48$; experimental increased effort: males, $r_{24} = 0.19$, $P = 0.37$; females, $r_{28} = 0.03$, $P = 0.86$).

Overall, there was a differential effect of treatment by sex (Fig. 4; treatment × sex: $F_{1,101} = 10.43$, $P = 0.002$). Thus, males did not decrease their body mass in response to brood enlargement, or to handicapping. In contrast, females decreased their own condition in response to their handicap, partner's handicap and brood enlargement. However, there were no significant differences between experimental females according with the treatment; females had a similar body mass in the three experimental groups (handicap female group 1891 ±

45 g; handicap male group 1897 ± 25 g; brood enlarged group 1902 ± 28 g; Fig. 4). This suggests that females decreased their condition until a fixed lower limit.

Discussion

We showed that in blue-footed boobies the sexes reacted differentially to being handicapped. In handicapped males condition remained stable, while in handicapped females condition deteriorated (Fig. 4; Velando 2002). The mass loss of handicapped females could be an adaptive response to compensate for the increase in their flight costs (see Norberg 1981; Pennycuick 1989). In fact, some bird species lose mass abruptly at the onset of the nestling phase to increase their efficiency in transporting food to their chicks (Moreno 1989; Jones 1994). However, that is not the case for blue-footed boobies, which maintain stable their body mass throughout the reproductive cycle (Wingfield *et al.* 1999; Velando 2002). In addition, the reduction of female body mass as a response to a handicapped partner and brood enlargement suggest that low body mass of experimental females represents energy stress associated with parental investment (Golet & Irons 1999). Reduction in body condition may be interpreted as an increase in reproductive costs (Drent & Daan 1980), which may reduce their long-term physiological condition (as for the immune system, e.g. Alonso-Alvarez & Tella 2001) and thereby their residual reproductive value, through elevated mortality or reduced future reproductive success (Golet *et al.* 1998; Wernham & Bryant 1998). We did not test for survival or fecundity costs across years, but in birds brood size manipulations that have demonstrated effects on adult condition have also often shown effects on adult residual reproductive value (review in Golet *et al.* 1998). Handicapping experiments and brood enlargement experiment had a strong effect on chick mass, indicating a reduction of parental effort. Seabird species exhibit positive correlations between mass at fledging and subsequent survival and lifetime reproductive success (Perrins, Harris & Britton 1972; Jarvis 1974; Spear & Nur 1994; but see Harris & Rothery 1985).

SEX DIFFERENCES IN BODY MASS REGULATION

The fact that males and females responded differentially in each of three different manipulations and their coincident pattern (Fig. 4) are fascinating findings. This different response suggests that costs or benefits of mass regulation differ between sexes (see Winkler 1987). Females compensated partially the reduced contribution of their partner. A compensatory response protects the chicks from detrimental effects of reduction in the amount of food delivered to the brood. In addition, females shared with the offspring the cost of being handicapped (Velando 2002), and also reduced their body mass in response to brood enlargement. This suggests that females can regulate their effort in relation to

offspring needs, conveyed probably through the chick's begging behaviour (Drummond 2002). In our study, males did not reduce their body condition as a response to handicap manipulation or to compensate for their partner's lower parental care, although the power of our tests was low. We did not measure directly male reproductive effort, but offspring and female partners reduced their body mass in the male handicapping experiment, which seems to suggest that males reduced their contribution. Males also did not reduce their body condition as a response to brood enlargement but increased their body condition when the brood was reduced. Thus, these results as a whole suggest that males work at some physiological maximum or are unwilling to pay the cost in terms of future survival when the cost of reproduction is increased.

The differences in body mass regulation agree with the differential provisioning pattern by male and female blue-footed boobies, a species where females are larger than males. Thus, Guerra & Drummond (1995) showed that male food contribution increases gradually until chicks are 10 days old, after that remaining constant, while female food contribution increases continuously during chick growth (at least until chicks are 35 days old). Thus, females seem to have a flexible parental effort according to the chicks' needs, whereas males have a fixed contribution after chicks are 10 days old. Like males, females probably have an upper limit but they could be working with a buffer of nutritional reserves. Several hypotheses can be proposed to explain this differential body mass regulation. (1) Long-lived seabirds can accumulate fat as energy reserves for self-maintenance (Cherel, Leloup & Le Maho 1988). Female blue-footed boobies are 31% heavier than males and females may have more stored fat than males. (2) Male may also deplete their reserves earlier due to previous investments in nest and territory defense (see Nelson 1978). (3) Moreover, in the blue-footed booby, it has been suggested that males and females differ in their foraging areas (Nelson 1978) and female boobies could be better foragers than males (Anderson & Ricklefs 1992) which could, in turn, influence the factors that govern energy allocation as occurs in wandering albatrosses, *Diomedea exulans* (Weimerskirch *et al.* 1997). (4) Another potential explanation is that future reproductive success differs between sexes, but there are no data on sex-specific fitness. (5) Lastly, in the blue-footed booby extra-pair copulations represent 13·3% of copulations by all females (Osorio-Beristain & Drummond 1998), and males may be careful in their parental effort decisions due to uncertainty of paternity. Despite the above explanations, the generality of differential response to manipulations between sexes remains to be explored, as already pointed out by Moreno *et al.* (1995).

CLUTCH SIZE AND PARENTAL CONDITION

Blue-footed boobies in this and most other populations rarely lay three eggs (Nelson 1978; A. Velando,

Table 2. Results of experiments that increased or reduced the reproductive effort and that have measure adult body condition and/or survival in seabird species. n = number of fledglings; C = body condition of fledglings; M = male parent; F = female parent; P = parents with sex not determined. Positive, negative and zero effects are indicated by +, – and 0, respectively

| Experiment/species | Offspring | | Parents | | | | | | Author |
| | N | C | Condition | | | Survival | | | |
			M	F	P	M	F	P	
Increased effort									
Brood enlarged									
Puffinus puffinus	–	–	0	0					Harris (1966)
Sula capensis	+	–			0				Jarvis (1974)
Sula nebouxii	+	–	0	–					This study
Larus glaucescens			–	–					Reid (1987)
Rissa tridactyla	0	–	0	–		0	–		Jacobsen *et al.* (1995)
Larus furcatus	0				0				Harris (1970)
Adult handicapped									
Diomedea chlororynchos[1]	0	–			–			0	Weimerskirch *et al.* (2000)
Pachyptila belcheri[1]	0	–			–				Weimerskirch *et al.* (1995)
Pachyptila desolata[1]	–				0				Weimerskirch *et al.* (1999)
Oceanodroma leucorhoa[1]	0	–			0				Mauck & Grubb (1995)
Thalassoica antartica[2]	–	–			0				Sæther *et al.* (1993)
Female handicapped									
Thalassoica antartica[3]	–			–					Tveraa *et al.* (1997)
Sula nebouxii	0	–	0	–					Velando (2002)
Male handicapped									
Sula nebouxii	0	–	0	–					This study
Partner removed									
Pachyptila belcheri	0	–			0				Weimerskirch *et al.* (1995)
Nestling period increased									
Fratercula arctica	–	–			–				Johnsen *et al.* (1994)
Reduced effort									
Brood reduced									
Sula nebouxii	–	0	+	0					This study
Rissa tridactyla	0	+	0	+		0	+		Jacobsen *et al.* (1995)
Clutch removed									
Rissa tridactyla			+	+		+	+		Golet *et al.* (1998); Golet & Irons (1999)
Chicks food-supplemented									
Calonectris diomedea	0	+			0				Hamer & Hill (1994)
Fratercula arctica	+	+	0					0[4]	Wernham & Bryant (1998)
Nestling period reduced									
Fratercula arctica	0	0			0				Johnsen *et al.* (1994)

[1]Both adults handicapped. [2]One adult handicapped but the sex was not determined. [3]Handicap experiment during the incubation. [4]Increased fecundity in the year following to manipulation.

unpublished data), despite their ability to brood experimental extra fledglings, as other Sulids (Nelson 1966; Jarvis 1974). Nevertheless, offspring from enlarged broods have lower body mass that can affect their fitness (Lindström 1999). Mothers should lay the clutch size that maximizes the number of new recruits in the population (Lack 1966; Perrins & Moss 1975). In addition, each female can have her own optimal clutch size depending on her particular situation (individual optimization hypothesis; Perrins & Moss 1975; Pettifor, Perrins & McCleery 1988). In long-lived birds, females' optimal decision should depend on their safety margin regarding their critical physiological condition. We found some evidence that the parental ability of boobies that naturally laid different number of eggs differed. Parents rearing unmanipulated broods had similar condition at the end of the experiment independently of their initial brood size, but males with two-egg clutches that were reduced to one nestling had better condition than those of natural broods with one or two

nestlings (Fig. 3). This suggests that, at least, males with two-egg clutches were able to allocate more resources to reproduction than males with one-egg clutches.

In addition to their own quality, females should adjust their clutch size to the quality of their mate. In seabirds, there is some evidence that parents are able to exchange information about their current body condition (Tveraa *et al.* 1997). Whether females adjust clutch size to male quality remains an open question, but it should be taken into account in species with sex-specific optimal clutch size.

REGULATION OF PARENTAL INVESTMENT AND BODY MASS THRESHOLD

The present results suggest that reproduction is costly for adult blue-footed boobies. Results of experimental studies on reproductive costs of seabird species are summarized in Table 2. From 23 experiments reporting adult condition or survival the results are mixed, with

65% finding some cost in adults. Although experimental designs varied widely, general trends can be detected in these experiments. No experiment showed that the experimentally imposed cost is paid only by parents, and only one study did not find any cost in offspring or parents (Harris 1966). Thus, most of the studies showed that the cost is passed to offspring or shared. In the blue-footed booby male costs of reproduction were detected, in terms of body condition, when effort was experimentally reduced, whereas female costs were evident when effort was increased experimentally. Also, some studies detected parental costs but other failed to demonstrate reproductive costs in the same species (Table 2). The failure in detecting parental cost in some experiments might have resulted from a reduced parental effort due to their body condition regulation. The reduced condition of nestling resulted from experiments where the parental effort was increased provides clear evidence that parents are restricted in the amount of food that they can supply to the young. Therefore, the inability of some studies to detect parental costs should be not used as evidence that reproduction is cost-free (Golet *et al.* 1998; Wernham & Bryant 1998; Tammaru & Hörak 1999).

The results of Table 2 suggest that seabirds are restrictive in the increase of parental effort. In some cases, parents may compensate for the increase in chick demand, although this compensation seems to be limited. Thus, for instance, in the Antarctic petrel (*Thalassoica antarctica*) the ability of parents to adjust their effort is dependent on their own condition (Tveraa *et al.* 1998), and during incubation the parents deserted the egg when their body mass reached some critical lower threshold (Tveraa *et al.* 1997). A critical body mass level also probably regulates parental desertion during incubation and the reduction in parental effort during the chick stage in many seabirds (Monaghan *et al.* 1989; Monaghan *et al.* 1992; Chaurand & Weimerskirch 1994; Olsson 1997; Weimerskirch 1998).

In Isla Isabel, blue-footed bobbies deserted their nests but maintained their body mass during the El Niño event of 1992 (Wingfield *et al.* 1999). In our studies, we showed that female boobies decreased their own body mass until a certain common mass level. In the three experiments with increased costs, females reached very similar values of body mass (Fig. 4), whereas offspring suffered differentially between experiments (Figs 1 and 3; Velando 2002). This suggests that females are working with a buffer of nutritional reserves at this critical level, and that below this level, females preferentially allocated resources to the maintenance of their body condition at the expense of investment in current reproduction. Our study was conducted during a good breeding season; females can use their nutritional reserves without compromising their future survival due to the good food availability (e.g. Weimerskirch *et al.* 2000, 2001) or alternatively, females can risk some of their future survival in order to produce young which would have better chances of survival (Erikstad *et al.* 1998).

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