

Sex-specific patterns in baseline corticosterone and body condition changes in breeding Red-footed Boobies *Sula sula*

HERVE LORMÉE,^{1*} PIERRE JOUVENTIN,² COLETTE TROUVE¹ & OLIVIER CHASTEL¹

¹Centre d'Etudes Biologiques de Chizé, CNRS, F-79360 Beauvoir sur Niort, France

²Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 Route de Mende, F-34293, Montpellier Cedex, France

Plasma levels of corticosterone often mirror changes in body condition and parental effort. In seabirds, the brooding of young chicks is often paralleled by a marked decline in adult body condition. This may reflect the trade-off between the needs of the chick to be fed regularly and brooded, and that of the adult to spend enough time at sea to restore its body reserves and find food for the chick. In this paper, we describe changes in body condition and baseline corticosterone levels in a tropical seabird, the Red-footed Booby *Sula sula*, in which the chick is continuously brooded for 5–6 weeks. Body condition did not decline during the brooding period. Female body condition remained stable throughout breeding whereas male body condition declined significantly during the late chick-rearing period. Baseline corticosterone levels were low during the prelaying phase, increased significantly during incubation and were highest during the brooding period. Later in the chick-rearing period, baseline corticosterone levels decreased markedly in females, but stayed elevated in males. There was no correlation between baseline corticosterone and body condition. Because of the chick's slow growth and reduced daily need for food, brooding in Red-footed Boobies may not require a marked increase in parental effort, and the rise in corticosterone levels is probably more a reflection of slight changes in foraging activity. Red-footed Booby males are 15% smaller than females and we suggest that the decline in male body condition during the late chick-rearing period is likely to result from higher energetic flight costs or a lower foraging efficiency imposed by a smaller body size.

The reproductive cycle in birds involves a complex sequence of behaviours such as territory establishment, courtship, incubation and chick rearing. During these successive reproductive stages, adult birds have to cope with different energetic constraints, and corticosterone secretion is one of the physiological means through which homeostasis is maintained (Wingfield 1994). The elevation of plasma corticosterone titres under periods of reduced food availability allows the mobilization of energy stores via protein catabolism (Cherel *et al.* 1988), and simultaneously enhances foraging behaviour and feeding (Wingfield 1988, Astheimer *et al.* 1992). If suboptimal environmental conditions persist, elevated corticosterone levels can lead to nest desertion (Wingfield

1988). In such a context of energetic stress, the rise in corticosterone levels is associated in many species with a decrease in adult body condition (Wingfield & Farner 1979, Silverin & Wingfield 1982, Wingfield 1984, Dufty & Wingfield 1986, Meijer & Schwabl 1989, Holberton *et al.* 1996, Schoech *et al.* 1997, Kitaysky *et al.* 1999), but not at all times and in all bird species studied (Cherel *et al.* 1988, Schwabl 1995, Silverin *et al.* 1997, Hood *et al.* 1998, Silverin & Wingfield 1998).

During the breeding season, pelagic seabirds have to commute from remote feeding areas to nesting colonies, and throughout the successive breeding stages, adults face variable energetic constraints. For example, the transition from egg incubation to the brooding of thermally dependent chick requires an increase of parental effort because adults face a trade-off between the needs of the chick to be regularly fed

*Corresponding author.
Email: h.lormee@oncs.gouv.fr

and brooded, and that of the adult to spend enough time at sea to restore its body reserves and find food for the chick. Thus, the brooding of a young chick can reduce feeding opportunities for the adults and, accordingly, brooding seabirds often experience a significant decline in body condition around the time of hatching (Weimerskirch 1990, Tveraa *et al.* 1998).

An increase of parental effort has been shown to be associated with elevated corticosterone titres in some bird species (Silverin 1982, Kitaysky *et al.* 1999). In seabirds, the simultaneous changes in baseline corticosterone and body condition have been studied mainly during incubation (Cherel *et al.* 1988, Hector & Harvey 1986, Hood *et al.* 1998), when the longest periods of fasting occur. However, the few seabird species in which changes in body condition and corticosterone values have been investigated during the entire breeding cycle show variation in patterns (Kitaysky *et al.* 1999, Wingfield *et al.* 1999, Lormée *et al.* unpubl. data). Distinct differences in parental care, particularly during the chick-rearing period, may provide a clue to understanding the source of variation in the pattern of changes in body mass and baseline corticosterone values. To understand the interactions between body condition and corticosterone we must enlarge the range of species studied, to include seabirds that have different patterns of parental care and therefore differ in the energetic constraints that they support during breeding.

Tropical Pelecaniformes such as tropicbirds (*Phaethon* spp.), boobies (*Sula* spp.) or frigatebirds (*Fregata* spp.) have a very long reproductive season due to slow chick growth (Nelson 1983). In Red-footed Boobies (*Sula sula*), the single egg is incubated for 45 days and the chick is brood-guarded continuously for 5–6 weeks (Nelson 1978). Thereafter, the chick is left alone at the nest for most of the time, but fed by the parents for a further 60 days (Nelson 1978). The whole parental phase (incubation and chick stage) lasts for 145 days and is followed by post-fledging care for more than 1 month (Nelson 1978).

To understand better the relationships between variation in baseline corticosterone levels and variation in body condition in seabirds, we measured changes in baseline corticosterone levels and body condition in the Red-footed Booby, during breeding, to examine how the successive breeding stages affected these changes. We investigated whether the long brood-guard period was associated with a marked depletion in body mass and a rise in corticosterone levels.

Furthermore, Red-footed Boobies exhibit a marked reversed sexual size dimorphism, females being 15% larger than males (Lormée & Chastel unpubl. data). Growing evidence suggests that reversed sexual size dimorphism in tropical Pelecaniformes is associated with a sex difference in parental effort (Anderson & Ricklefs 1992, Guerra & Drummond 1995, Osorno 1996, Lormée & Chastel unpubl. data), and hormone secretion patterns (Lormée *et al.* 2000). We therefore examined whether baseline corticosterone levels, changes in corticosterone levels, and body condition throughout the successive stages of breeding differed between males and females.

METHODS

Study area and birds

The study was conducted from 3 September to 14 October 1998 (breeding season) and from 9 to 21 March 1999 (non-breeding season), on Europa Island (22°20'S, 40°22'E), Mozambique Channel, Western Indian Ocean, where large numbers of Red-footed Boobies breed (3000–4000 pairs, Le Corre & Jouventin 1997). Red-footed Boobies nest in trees and lay a single egg, which is incubated equally by both parents for 45 days (Nelson 1978, H. Lormée unpubl. data). The thermally dependent chick is brooded for approximately 15–20 days (Nelson 1978, H. Lormée pers. obs.). Thereafter, the chick is continuously guarded until *c.* 30–40 days (H. Lormée pers. obs.; Schreiber *et al.* 1996). The chick fledges at about 100 days but post-fledging care can extend the chick-rearing period until about 130 days (Nelson 1978).

Body condition

Birds were captured on the nest by hand or with a landing net, and ringed with a metal ring. To estimate body size, we measured the length of tarsus with callipers (± 0.1 mm), wing length with a steel rule (± 1 mm) and body mass with a *Pesola* balance (± 5.0 g). H. Lormée performed all measurements. Body mass was best correlated with tarsus length in females ($r_{59} = 0.42$, $P = 0.001$, and 18% of the variance in body mass was explained by tarsus length), and with wing length in males ($r_{56} = 0.35$, $P = 0.007$, and 12% of the variance in body mass was explained by wing length). Body condition index was therefore expressed as the residual mass from a

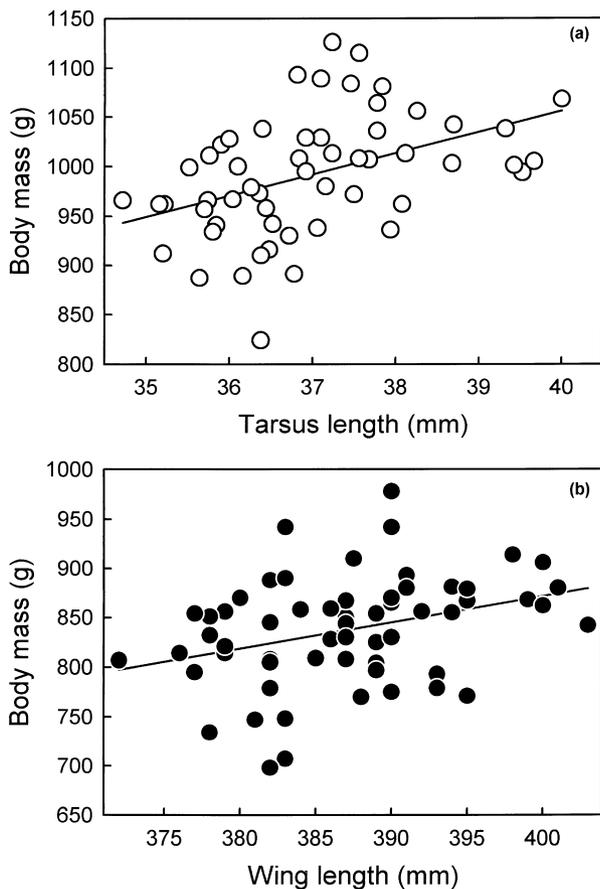


Figure 1. Relationship between (a) body mass and tarsus length in female Red-footed Boobies (white dots); line equation: $\text{Mass} = 21.37 \times \text{Tarsus length} + 200.95$ and (b) body mass and wing length in male Red-footed Boobies (black dots); line equation: $\text{Mass} = 2.64 \times \text{Wing length} - 187.3$.

linear regression relating body mass to body size (equation for females: $\text{Mass} = 21.37 \times \text{Tarsus length} + 200.95$, Fig. 1a; equation for males: $\text{Mass} = 2.64 \times \text{Wing length} - 187.3$, Fig. 1b). Thus defined, body condition is expressed as a size-corrected body mass in grams.

Blood sampling

Blood samples were collected throughout the breeding period which was divided into five reproductive stages: (1) non-breeding: adults found within the colony and not engaged in any reproductive activity; (2) prelaying, which includes the copulation and nest building periods; (3) incubation; (4) brooding of the thermally dependent chick; (5) rearing of the large, thermally independent chick. Red-footed

Boobies are tame birds that are easily approached at the nest. After the blood sampling, birds were returned to the nest. Most birds immediately resumed parental care; some birds flew after release but were back 2–5 min after blood sampling. At Europa Island, Red-footed Boobies are loosely colonial and typically nest in clusters of 1–8 nests. To reduce possible disturbance to nearby breeders during the blood sampling of an individual, only one bird was sampled within a cluster and we selected isolated nests in our study plot. Because Red-footed Boobies have a loosely seasonal breeding pattern on Europa Island (Le Corre 2001), all breeding stages were found simultaneously and we therefore were able to sample each breeding stage at any time during the 41-day study period. Blood samples were taken between 07:30 h and 17:30 h. Because we were studying other hormones as well (Lormée *et al.* 2000), we collected approximately 1 mL of blood (range 0.3–2 mL) from the tibial vein into heparinized tubes. Blood samples were collected within a range of 2–16 min after the initial disturbance of the bird ($n = 143$). Samples were placed on ice and centrifuged as soon as possible. Afterwards, plasma was removed and stored at -20°C until assayed.

Sexing

When captured, Red-footed Boobies can be sexed easily using voice upon capture (Nelson 1978, Lormée *et al.* 2000). The use of voice to sex the birds has been validated previously through a molecular method (Lormée *et al.* 2000). Additionally, some birds were sexed using behavioural observations (laying, copulation).

Hormone assays

Corticosterone levels were determined at the CEBC following the procedure of Mauget *et al.* (1994) for steroid hormones. Plasma corticosterone was measured in samples (30 μL) after ethyl ether extraction by radioimmunoassays using a commercial anti-serum, raised in rabbits against corticosterone-3-(O-carboxy-methyl) oxime bovine serum albumin conjugate (Biogenesis, UK). Cross-reaction was 9% with 1-desoxycorticosterone and less than 0.1% with other plasma steroids. Duplicate aliquots (100 μL) of the extracts were incubated overnight at 4°C with 8000 cpm of ^3H -Corticosterone (Amersham Pharmacia Biotech-France) and antiserum. The

bound and free corticosterone were separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. Minimal detectable corticosterone levels were 0.4 ng mL^{-1} (lowest measurement: 1.26 ng mL^{-1}). All samples were run in three assays; the coefficients of intra- and interassay variation were assessed using several reference plasma within each and separate assays, and were 8.2 and 10.9%, respectively.

Statistical analysis

Statistical analyses were performed using SYSTAT 7.0 (Wilkinson 1997). All statistical tests are two-tailed, and probability levels < 0.05 were considered significant. Values are presented as means \pm standard error. Both hormone and body mass data showed a normal distribution, but to homogenize variance, all body condition and corticosterone values were log transformed. To avoid pseudoreplication, birds were represented only once in the whole data set.

In birds, corticosterone levels increase rapidly in response to acute stress of capture and handling (Wingfield *et al.* 1999). Blood samples ($n = 143$) were collected 2–16 min after capture. To make sure that values were close to and representative of baseline corticosterone levels, we first analysed relationships between corticosterone levels and handling time through a GLM, with handling time and sex as factors. Corticosterone levels increased with handling time ($F_{1,139} = 20.12$, $P < 0.001$), with no effect of sex ($F_{1,139} = 0.73$, $P = 0.39$; interaction sex \times handling time: $F_{1,139} = 0.46$, $P = 0.50$). Because adrenocortical response to stress can differ between breeding stages (Kitaysky *et al.* 1999), we then analysed the effect of handling time on corticosterone levels for each breeding stage through a regression analysis. If the regression was significant, we then removed the data until the regression was no longer significant. The time interval during which there was no significant effect of handling time on corticosterone secretion was considered close to and representative of baseline corticosterone levels. Corticosterone values were not affected by handling time in samples collected within 3 min in non-breeding birds ($P = 0.3$, three samples removed), within 6.25 min in prelaying birds ($P = 0.89$, six samples removed), within 6.25 min in incubating birds ($P = 0.62$, 13 samples removed), within 6.5 min in chick-brooding birds ($P = 0.33$, seven samples removed), and within 6.25 min in chick-rearing birds ($P = 0.20$, eight samples removed).

To check for diel variation in corticosterone levels and BCI, we regressed, within each reproductive stage, baseline corticosterone values against the hour when the bird was captured. No effect of the hour of capture was detected for either variable. Because we sampled birds at any time of their fasting bouts, we checked to see if baseline corticosterone levels significantly differed between birds starting or finishing a fasting spell on the nest. Birds sampled early in the morning (early: 07:00 h to 10:00 h) were beginning an incubation or brooding bout whereas those sampled in late afternoon (late: 16:00 h to 19:00 h) were ending their stay on the nest. Using a one-way ANOVA (time of the day as the main factor: early vs. late), we detected no significant difference in baseline corticosterone between early and late captures. We first studied changes in baseline corticosterone values and body condition between the non-parental (non-breeding and prelay) and the parental phase (incubation, brooding and rearing) using a one-way ANOVA with phases (parental or non-parental) as the factor, followed by *post hoc* Tukey tests. To study the effects of sex and breeding stages on hormone and body condition values within the parental phase, we used a two-way ANOVA, with sex and breeding stages as factors, followed by *post hoc* Tukey tests. We used Pearson correlation to investigate the relationship between body condition and baseline corticosterone, using log-transformed values.

RESULTS

Body condition

On average, body condition during the non-parental and the parental phases was similar ($F_{1,138} = 0.001$, $P = 0.97$; Fig. 2). During the parental phase, body condition changed, following a different pattern between males and females (sex \times breeding stage, $F_{2,111} = 4.34$, $P = 0.015$). Female body condition stayed unchanged throughout breeding. In contrast, the body condition of males was lower during rearing compared to brooding (Tukey test: $P < 0.001$), and incubation (Tukey test: $P < 0.001$).

Baseline corticosterone levels

On average, baseline corticosterone levels found during the parental phase were much higher than those found during the non-parental phase ($F_{1,104} = 89.27$, $P < 0.001$; Fig. 3). During the parental phase, baseline corticosterone levels changed significantly across

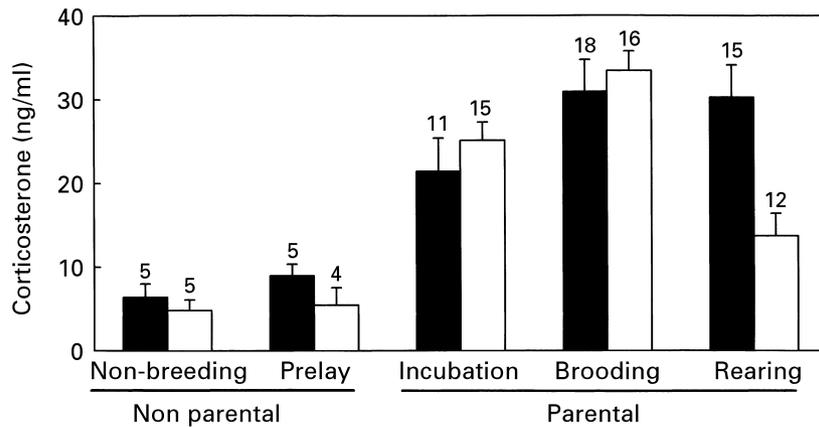


Figure 2. Body condition in male (solid bars) and female (open bars) Red-footed Boobies in relation to reproductive stage. Shown are means \pm se. Sample sizes are given above the bars.

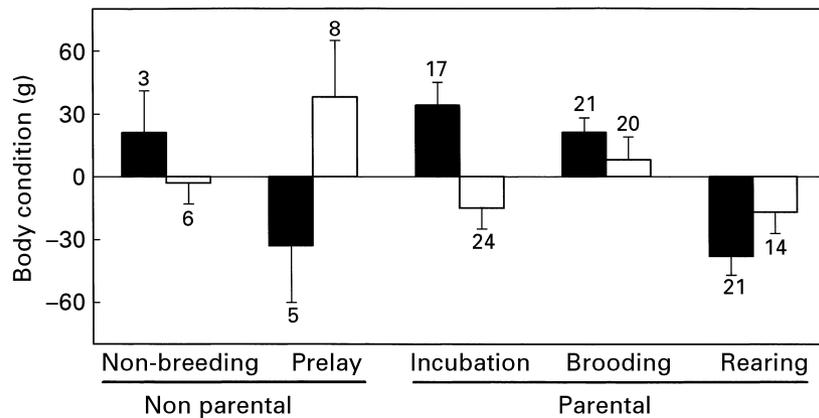


Figure 3. Baseline corticosterone levels in male (solid bars) and female (open bars) Red-footed Boobies in relation to reproductive stage. Shown are means \pm se. Sample sizes are given above or below the bars.

breeding stages ($F_{2,81} = 6.86$, $P = 0.002$), increasing from incubation to brooding (Tukey test: $P = 0.036$) and, on average, did not differ between sexes ($F_{1,81} = 2.26$, $P = 0.136$). However changes in baseline corticosterone levels across breeding stages differed between sexes (sex \times breeding stage: $F_{2,81} = 7.077$, $P = 0.001$; Fig. 3): from brooding to rearing, corticosterone values decreased in females (Tukey test: $P < 0.001$) but stayed elevated in males (Tukey test: $P = 0.99$).

Relationship between corticosterone and body condition

On average, there was no correlation between corticosterone values and body condition in males (Pearson correlation; $n = 51$, coefficient = -0.22 , $P = 0.12$) and females (Pearson correlation; $n = 52$,

coefficient = -0.04 , $P = 0.78$). We also checked for this relationship at every stage of parental phase. We detected no significant correlation between corticosterone levels and body condition, with the only exception being that there was a suggestion of a negative relationship in brooding males (Pearson correlation; $n = 18$, coefficient = -0.41 , $P = 0.09$).

DISCUSSION

Body condition

In several seabirds, adults undergo a marked decline in body condition during the first part of the nestling period and lose 4–18% of their incubation body mass during the brooding stage (Croll *et al.* 1991, Jones 1994, Phillips & Furness 1997, Bech *et al.* 1999,

Weimerskirch & Lys 2000). This post-hatching decline has been interpreted as either the consequence of reduced feeding opportunities imposed by the brooding activity (Weimerskirch & Lys 2000, Tveraa *et al.* 1998) or as an adaptive adjustment of body reserves to reduce flight costs to attain the optimal body mass required for a high food provisioning effort later in the nestling period (Freed 1981, Croll *et al.* 1991, Jones 1994).

In Red-footed Boobies, however, despite an extended brooding period, body condition does not decrease and shows little or no variation during the whole breeding cycle. Further, the decline in male body condition occurs after the brooding period, later in the nestling period than in other seabirds. This constancy in body mass is also found in another tropical sulid, the Blue-footed Booby *Sula nebouxii* (Wingfield *et al.* 1999). Tropical booby chicks have a very slow growth and thus reduced daily needs of food (Nelson 1978), and adults do not have to fatten the chick before it fledges (Ashmole 1971, Ricklefs 1990). After hatching, seabirds often dramatically reduce the length of foraging trips and increase the visit frequency to the nest (e.g. Weimerskirch & Lys 2000). In Red-footed Boobies, however, probably due to the low daily need of food of the chick, the duration of foraging trips only decreases from 11.2 ± 0.48 h during incubation to 7.5 ± 0.50 h after hatching (Lormée & Chastel unpubl. data). This probably represents a modest reduction in self-feeding opportunities for the adult and this may have few or no consequences for adult body condition. Considering the adaptive mass loss hypothesis (Freed 1981), parent Red-footed Boobies are probably not forced to adjust their body mass after hatching because of the low food requirement of the chick.

Baseline corticosterone levels

Changes in baseline corticosterone levels often mirror changes in body reserves (Cherel *et al.* 1988). For example, in Black-legged Kittiwakes *Rissa tridactyla*, baseline corticosterone levels rose steadily while breeding; this was associated with a marked decline in body condition (Kitaysky *et al.* 1999). In the Red-footed Booby, despite few changes in body condition (especially in females), baseline corticosterone levels showed a significant four-fold increase from the non-parental phase to the brooding stage. Similarly, in the Blue-footed Booby, baseline corticosterone tended to increase during the parental phase ($P = 0.07$) whereas body mass remained stable (Wingfield *et al.*

1999). Such an independence of corticosterone secretion to change in body condition has also been reported in the Pied Flycatcher *Ficedula hypoleuca* where an increase in provisioning effort was paralleled by an increase in baseline corticosterone levels but without change in adult body condition (Silverin 1982). This has been interpreted as the consequence of a more intense begging by nestlings in large broods, leading to higher corticosterone levels inducing an increase in the foraging effort of the parent (Silverin 1982). An increase in foraging activity, i.e. hyperphagia and searching for food, is one of the short-term effects of increased baseline corticosterone (Nagra *et al.* 1963, Wingfield & Silverin 1986, Gray *et al.* 1990, Schwabl *et al.* 1991, Astheimer *et al.* 1992, Holberton *et al.* 1996). This may also apply to boobies; that is, the increase in corticosterone titres from the non-parental to the parental phase probably reflects the higher foraging activity imposed by parental activities. Like Masked Boobies *Sula dactylatra* in the Galapagos (Anderson & Ricklefs 1992), Red-footed Boobies on Europa Island are diurnal foragers and therefore have a maximum of roughly 13 h per day to forage. During incubation, adults forage for 11–13 h per day to sustain fasting during their incubation shift, but after the chick hatches they reduce the duration of foraging trips slightly. On Europa, young chicks cannot be left unprotected because of the predation risk from Pied Crows *Corvus albus* (Le Corre & Jouventin 1997). Consequently, a successful breeding attempt requires co-ordination of brooding shifts. This limits the time an individual can forage, and probably implies a higher foraging effort per unit time. The elevated corticosterone levels found during the brooding stage may then reflect the increase in foraging activity for the parent that has to find food for the chick and for itself in less time.

Sex-specific patterns

This study revealed a sex-specific pattern in body condition and baseline corticosterone changes. After the brooding period, male body condition declined significantly during the rearing period in association with the maintenance of elevated corticosterone levels. On the other hand, female body condition remained stable and baseline corticosterone levels declined after the brooding period. This suggests that males and females might not provide similar amounts of parental care and probably face different energetic constraints.

Although females spend more time brooding the young chick during the day, male and female Red-footed Boobies broadly share parental care at the nest (Lormée & Chastel unpubl. data). However, the regulation of foraging trip duration differs between sexes: males spend more time at sea than females for an equivalent amount of time spent at the nest (Lormée & Chastel unpubl. data). This, and data obtained on Masked and Blue-footed Boobies (Anderson & Ricklefs 1992), suggests that male boobies may be less efficient foragers than females. Male Red-footed Boobies are 15% smaller than females and as the rate of energy expenditure per unit mass declines with increasing body mass (Peters 1983), one might expect that smaller males would use relatively more energy than larger females during their foraging trips and, consequently, would need more time to forage for the chick and for themselves (Barbraud *et al.* 1999). Males may then endure more energetic constraints, which in turn, would negatively affect their body condition. Since we observe no correlation between baseline corticosterone levels and body condition in males, the elevated corticosterone levels found throughout the chick-rearing period may, rather, reflect a higher and sustained foraging effort in males.

After the brooding period, when the chick can be left alone, the higher foraging efficiency of females probably allows them to lower their foraging effort per unit time and to maintain a stable body mass. This may be reflected by the observed decrease in baseline corticosterone levels. Such hypotheses need now to be tested further using precise metabolic measurements of the respective foraging effort of males and females.

This work was supported by the Direction Régionale de l'Environnement (DIREN – Ministère de l'Environnement) of Réunion Island and by a grant from the Ministère de la Recherche et de la Technologie. Visits to the islands were authorized by the Préfet de Réunion Island, and organized with the help of the Direction Régionale de MétéoFrance. We would like to thank its Director, Mr Soulan, and his staff on the island. Transport to Europa was made possible through collaboration of the Forces Armées de la Zone Sud de l'Océan Indien (FAZSOI). We are indebted to Mrs Sonia Ribes, curator of the Muséum d'Histoire Naturelle of Réunion Island, who helped us to conduct research on Europa and Tromelin islands. We also thank M. Kersten for field assistance, Z. Marillet for her excellent technical assistance, and M., C. and A. Le Corre for their help. L. Astheimer and B. Buttemer greatly improved an early draft of the manuscript. Finally, we thank two anonymous referees for their useful comments on the earlier draft of the manuscript.

REFERENCES

- Anderson, D.J. & Ricklefs, R.E. 1992. Brood size and food provisioning in Masked and Blue-footed Boobies (*Sula* spp.). *Ecology* **73**: 1363–1374.
- Ashmole, N.P. 1971. Seabird ecology and the marine environment. In Farner, D.S. & King, J.R. (eds) *Avian Biology*, Vol. 1: 224–286. New York: Academic Press.
- Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scand.* **23**: 355–365.
- Barbraud, C., Weimerskirch, H., Robertson, G.G. & Jouventin, P. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *J. Anim. Ecol.* **68**: 1179–1192.
- Bech, C., Langseth, I. & Gabrielsen, G.W. 1999. Repeatability of basal metabolism in breeding female kittiwakes *Rissa tridactyla*. *Proc. Roy. Soc., Lond.* **266**: 2161.
- Cherel, Y., Robin, J.P., Walch, O., Karmann, H., Netchitailo, P. & Le Maho, Y. 1988. Fasting in the King Penguin I: Hormonal and metabolic changes during breeding. *Am. J. Physiol.* **254**: R170–R177.
- Croll, D.A., Gaston, A.J. & Noble, D.G. 1991. Adaptive mass loss in Thick-billed Murres. *Condor* **93**: 496–502.
- Dufty, A.M. & Wingfield, J.C. 1986. Temporal patterns of circulating LH and steroid hormones in a brood parasite, the Brown-headed Cowbird, *Molothrus ater*. I. Males and II. Females. *J. Zool., Lond.* **208**: 191–203.
- Freed, L.A. 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* **62**: 1179–1186.
- Gray, J.M., Yarian, D. & Ramenovsky, M. 1990. Corticosterone, foraging behavior and metabolism in Dark-eyed Junco, *Junco hyemalis*. *General Comp. Endocrinol.* **79**: 375–394.
- Guerra, H. & Drummond, H. 1995. Reversed sexual size dimorphism and parental care: minimal division of labour in the Blue-footed Booby. *Behaviour* **132**: 479–496.
- Hector, J.A. & Harvey, S. 1986. Corticosterone secretion through long incubation shifts in *Diomedea* albatrosses. *General Comp. Endocrinol.* **62**: 349–352.
- Holberton, R.L., Parrish, J.D. & Wingfield, J.C. 1996. Modulation of the adrenocortical stress response in neotropical migrants during autumn migration. *Auk* **113**: 558–564.
- Hood, L.C., Boersma, P.D. & Wingfield, J.C. 1998. The adrenocortical response to stress in incubating Magellanic Penguins (*Spheniscus magellanicus*). *Auk* **115**: 76–84.
- Jones, I.L. 1994. Mass changes of Least Auklets *Aethia pusilla* during the breeding season: evidence for programmed loss of mass. *J. Anim. Ecol.* **63**: 71–78.
- Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. 1999. Dynamics of food availability, body condition and physiological response in breeding black-legged kittiwakes. *Funct. Ecol.* **13**: 577–585.
- Le Corre, M. 2001. Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. *J. Zool., Lond.* **254**: 239–250.
- Le Corre, M. & Jouventin, P. 1997. Ecological significance and conservation priorities of Europa island (Western Indian Ocean), with special reference to seabirds. *Terre et Vie* **52**: 205–220.
- Lormée, H., Jouventin, P., Lacroix, A., Lallemand, J. & Chastel, O. 2000. Reproductive endocrinology of tropical seabirds: sex-specific patterns in LH, steroids and prolactin

- secretion in relation to parental care. *General Comp. Endocrinol.* **117**: 413–426.
- Mauget, R., Jouventin, P., Lacroix, A. & Ishii, S.** 1994. Plasma LH and steroid hormones in king penguin (*Aptenodytes patagonicus*) during the onset of the breeding cycle. *General Comp. Endocrinol.* **93**: 36–43.
- Meijer, T. & Schwabl, H.** 1989. Hormonal patterns in breeding and non-breeding kestrels, *Falco tinnunculus*: field and laboratory studies. *General Comp. Endocrinol.* **74**: 148–160.
- Nagra, B.L., Breitenbach, R.P. & Meyer, R.K.** 1963. Influence of hormones on food intake and lipid deposition in castrated pheasants. *Poult. Sci.* **17**: 481–485.
- Nelson, J.B.** 1978. *The Sulidae: Gannets and Boobies*. Oxford: Oxford University Press.
- Nelson, J.B.** 1983. Contrasts in breeding strategies between some tropical and temperate marine Pelecaniformes. *Stud. Av. Biol.* **8**: 95–114.
- Osorno, J.L.** 1996. *Evolution of breeding behavior in the Magnificent Frigatebird: copulatory pattern and parental investment*. Unpublished PhD dissertation, Gainesville, FL, USA: University of Florida.
- Peters, R.H.** 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Phillips, R.A. & Furness, R.W.** 1997. Sex-specific variation in the loss of mass by breeding Arctic Skuas. *J. Avian Biol.* **28**: 163–170.
- Ricklefs, R.E.** 1990. Seabird life histories and the marine environment: some speculations. *Col. Waterbird* **13**: 1–6.
- Schoech, S.J., Mumme, R.L. & Wingfield, J.C.** 1997. Corticosterone, reproductive status, and body mass in a cooperative breeder, the Florida Scrub-Jay (*Aphelocoma coerulescens*). *Physiol. Zool.* **70**: 68–73.
- Schreiber, E.A., Schreiber, R.W. & Schenk, G.A.** 1996. Red-footed Booby (*Sula sula*). In Poole, A. & Gills, F. (eds) *The Birds of North America*, No. 241. Philadelphia: Academy of Natural Sciences, and Washington, D.C.: American Ornithologists' Union.
- Schwabl, H.** 1995. Individual variation of the acute adrenocortical response to stress in the White-throated Sparrow. *Zoology* **99**: 113–120.
- Schwabl, H., Bairlein, F. & Gwinner, E.** 1991. Basal and stress-induced corticosterone levels of Garden Warblers, *Sylvia borin*, during migration. *J. Comp. Physiol. B* **161**: 576–580.
- Silverin, B.** 1982. Endocrine correlates of brood size in adult Pied Flycatchers, *Ficedula hypoleuca*. *General Comp. Endocrinol.* **47**: 18–23.
- Silverin, B., Arvidsson, B. & Wingfield, J.C.** 1997. The adrenocortical responses to stress in breeding Willow Warblers *Phylloscopus trochilus* in Sweden: effects of latitude and gender. *Funct. Ecol.* **11**: 376–384.
- Silverin, B. & Wingfield, J.C.** 1982. Patterns of breeding behaviour and plasma levels of hormones in a free-living population of Pied Flycatchers, *Ficedula hypoleuca*. *J. Zool., Lond.* **198**: 117–129.
- Silverin, B. & Wingfield, J.C.** 1998. Adrenocortical responses to stress in breeding Pied Flycatchers *Ficedula hypoleuca*: relation to latitude, sex and mating status. *J. Avian Biol.* **29**: 228–234.
- Tveraa, T., Saether, B.-E., Aanes, R. & Erikstad, K.E.** 1998. Body mass and parental decisions in the Antarctic petrel: how long should the parents guard their chick? *Behav. Ecol. Sociobiol.* **43**: 73–79.
- Weimerskirch, H.** 1990. Weight loss of Antarctic Fulmars *Fulmarus glacialis* during incubation and chick brooding. *Ibis* **132**: 68–77.
- Weimerskirch, H. & Lys, P.** 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biol.* **23**: 733–744.
- Wilkinson, L.** 1997. *Systat 7.0 New Statistics*. Chicago: SPSS Inc.
- Wingfield, J.C.** 1984. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. I. Temporal organization of the breeding cycle. *General Comp. Endocrinol.* **56**: 406–416.
- Wingfield, J.C.** 1988. Changes in reproductive function of free-living birds in direct response to environmental perturbations. In Stetson, M.H. (ed.) *Processing of Environmental Information in Vertebrates*: 121–148. Berlin: Springer-Verlag.
- Wingfield, J.C.** 1994. Modulation of the adrenocortical response to stress in birds. In Davey, K.G., Peter, R.E., & Tobe, S.S. (eds) *Perspectives in Comparative Endocrinology*: 520–528. Ottawa: National Research Council of Canada.
- Wingfield, J.C. & Farner, D.S.** 1979. Some endocrine correlates of re-nesting after loss of clutch or brood in the White-crowned Sparrow, *Zonotrichia leucophrys gambelli*. *General Comp. Endocrinol.* **38**: 322–331.
- Wingfield, J.C., Ramos-Fernandez, G., Nuñez De La Mora, A. & Drummond, H.** 1999. The effects of an 'El Niño' southern oscillation event on reproduction in male and female Blue-footed Boobies, *Sula nebouxii*. *General Comp. Endocrinol.* **114**: 163–172.
- Wingfield, J.C. & Silverin, B.** 1986. Effects of corticosterone on territorial behavior of free-living male Song Sparrow, *Melospiza melodia*. *Horm. Behav.* **20**: 405–417.

Received 29 November 2000;
revised manuscript accepted 9 March 2002