



## Begging and provisioning of thin-billed prions, *Pachyptila belcheri*, are related to testosterone and corticosterone

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Vigorous begging is usually seen as an expression of parent–offspring conflict over limited resources. Chicks signal need by begging, but the evolution of honest signals requires the signals to be costly. Although some possible costs have been identified, the cost-inducing mechanisms underlying this widely distributed signalling system remain unclear. Because hormones associated with stress and hunger (corticosterone) and aggressive behaviour (testosterone) have deleterious side-effects, signalling costs may be coupled to the expression of such hormones, if they are closely associated with the signal. We tested whether begging in chicks of thin-billed prions (Aves, Procellariiformes) is associated with secretion of corticosterone and testosterone. Prion chicks honestly signalled their nutritional state. Begging increased with decreased body condition, both within and between chicks. Adults responded to more intense begging by delivering larger meals. Chick testosterone levels were positively correlated with measures of begging intensity and the mean body condition of chicks was correlated positively with testosterone and negatively with corticosterone. In a cross-fostering experiment, the change in testosterone and corticosterone between control and experimental periods was positively correlated with the change in begging intensity. This is the first experimental evidence that the control of chick begging by endogenously produced testosterone and corticosterone may form a mechanism controlling parental provisioning in birds, and that chick behaviour can help to explain the variation in growth patterns between individual birds.

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Avian nestlings commonly beg to obtain food from their parents and this has been used as a model to study parent–offspring conflict and the evolution of signalling (Mock & Parker 1997; Wright & Leonard 2002). Vigorous begging is usually seen as an expression of conflict over resource allocation between parents and offspring. When they beg, nestlings use vocal signals, gape colour and postural displays to transfer information about their nutritional state and health (Kilner 1997; Wright & Leonard 2002). The conflicting interests of parents and offspring about the

distribution of limited resources might lead to dishonest exaggeration of begging signals unless these signals are reined in by costs (Godfray 1995; Rodríguez-Gironés 1999). A number of possible costs have been identified (reviewed in Roulin 2001), including minimal energetic costs (Chappell & Bachman 2002), depressed growth rate (Kilner 2001; but see Leonard et al. 2003), and conspicuousness increasing the likelihood of predation (Haskell 2002; Platzen & Magrath 2004). However, the mechanisms underlying these observed effects remain to be identified. Hormones associated with stress and hunger (corticosterone) and aggressive behaviour (testosterone) have deleterious effects, so the costs of the signal may also be coupled with endocrine control, if these are associated with the signal. Negative effects of excessively elevated steroid hormones may include compromised immunocompetence (e.g. Peters 2000; Buchanan et al. 2003; Westneat et al. 2003; Naguib et al. 2004), increased metabolic rate (Buchanan et al. 2001) and compromised cognitive abilities (Kitaysky et al. 2003).

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The effects of hormones on begging behaviour of chicks have been studied in only a few avian species (summarized in Schwabl & Lipar 2002). Two types of steroid hormones influence begging behaviour: testosterone from mothers and corticosterone in chicks.

(1) Maternal hormones, including testosterone deposited in eggs, may influence begging behaviour in newly hatched chicks. Schwabl (1996) investigated the effect of maternal androgens on begging behaviour in canaries, *Serinus canaria*, and found that testosterone treatment increased the number of begging bouts, the total time spent begging and the duration of a begging bout within the first hour of hatching. Similarly, chicks of black-headed gulls, *Larus ridibundus*, that hatched from testosterone-injected eggs begged more frequently than controls (Eising & Groothuis 2003). This 'organizational hypothesis' (Schwabl & Lipar 2002) suggests that offspring behaviour can be manipulated by the mother through active allocation of hormones to the egg. There is, however, considerable potential for altricial nestlings to produce their own testosterone (Adkins-Regan et al. 1990), which may be particularly relevant for chicks with a long nestling period, such as tube-nosed seabirds.

(2) In black-legged kittiwakes, *Rissa tridactyla*, corticosterone-implanted chicks begged more frequently than sham-implanted controls (Kitaysky et al. 2001a, 2003), thus suggesting that corticosterone might provide a mechanistic link between the physiological condition of chicks and behavioural interactions with their parents. However, elevated corticosterone in black-legged kittiwake chicks was associated not only with increased food intake, but also with costs such as low growth efficiency and compromised cognitive abilities later in life (Kitaysky et al. 2003). These results suggest that juvenile physiological traits may be related to the fitness of birds in subsequent life history stages.

Most studies of begging have been carried out on passeriform birds, where nestlings are reared in the competitive environment of broods containing several individuals. This choice of subjects may pose a problem for the interpretation of data on resource allocation, because the begging signal intensity is determined by need as well as by the potentially confounding effect of sibling competition (Kilner & Johnstone 1997; Krebs 2001). Studies of begging in the absence of nestling competition may therefore provide especially useful models for the study of signalling interaction between parents and offspring.

The only avian order in which all species have an obligate clutch size of one is the Procellariiformes, which is therefore especially suitable for studying begging in the absence of sibling competition. In previous studies of procellariiform seabirds, begging rates significantly influenced meal sizes in Wilson's storm petrels, *Oceanites oceanicus* (Quillfeldt 2002), Manx shearwaters, *Puffinus puffinus* (Quillfeldt et al. 2004a) and Cory's shearwaters, *Calonectris diomedea* (Quillfeldt & Masello 2004). Furthermore, in Wilson's storm petrels, chicks with a low body condition index had increased levels of faecal corticosterone (Quillfeldt & Möstl 2003), a hormone that may stimulate begging behaviour.

Pelagic procellariiform seabirds provision their chicks less frequently than other birds do (e.g. Brooke 2004). The chicks accumulate large lipid reserves, attaining peak masses of up to 190% of adult mass. Chicks then lose mass and fledge at close to adult mass (Brooke 2004). The extreme patterns of provisioning and growth of pelagic seabirds have attracted considerable discussion. The main questions are how are provisioning rates regulated, and what explains the large differences between individual offspring. Most studies in this area have not analysed parent-offspring interactions (e.g. Ricklefs et al. 1985; Hamer & Hill 1994; Weimerskirch et al. 2000; but see Granadeiro et al. 2000; Quillfeldt 2002; Quillfeldt & Masello 2004; Quillfeldt et al. 2004a), and therefore have not adequately accounted for the influence of chick behaviour. However, several researchers have suggested that chicks often reject food and thus may have considerable influence on provisioning (e.g. Gray & Hamer 2001; Quillfeldt & Masello 2004).

We analysed hormonal regulation of chick behaviour in parent-offspring interactions in thin-billed prions. To explore the physiological basis of costly honest begging signals, we tested the following hypotheses: (1) chicks honestly signal their nutritional state to their parents and parents respond to begging by delivering larger meals; and (2) chick androgens and corticosterone covary with begging behaviour.

## METHODS

### Study Site and Species

The study was carried out in the New Island South Nature Reserve, Falkland Islands. We did the main part of the study from 8 January to 4 February 2003. Additional blood samples were taken in the 2003–2004 season, as described below.

Thin-billed prions breed in the Falkland Islands, Isla Noir (Chile), Crozet and Kerguelen but New Island is the most important known breeding site. Up to 2 million pairs were estimated to breed on this island in 2001–2002 (Catry et al. 2003). They are small nocturnal petrels, and the absence of adults from the nest burrow during the day provides the opportunity to collect data on chick provisioning with relatively little disturbance to the birds. Their life cycle and basic biology have been described by Strange (1980), and provisioning data from the 2003–2004 breeding season were analysed by Quillfeldt et al. (2003). Other studies of the biology of thin-billed prions have been carried out in Kerguelen, for example on sexual dimorphism of voice and morphology (Genevois & Bretagnolle 1995), feeding ecology (Chastel & Bried 1996; Cherel et al. 2002) and parental investment (Weimerskirch et al. 1995; Duriez et al. 2000).

Thin-billed prions show the typical procellariiform pattern of a single-egg clutch and slow chick development, with an average fledging period of 50 days (Strange 1980). They are burrow nesters, and we gained access to nests via short tunnels created in the roof of each burrow and capped with removable stone lids.

This system facilitated rapid access to chicks, reducing overall disturbance. Nests had been marked 3 years before our study. We checked them at the beginning of the season; if chicks were present we then monitored them daily. If eggs were present at our first visit we revisited the nests at the estimated hatching date (Quillfeldt et al. 2003).

### Chick Measurements

If chicks were present on our first visit, we determined their hatching dates ( $\pm 1$  day) by calibrating their wing length against wing growth in chicks of known age. Chicks were weighed daily ( $\pm 1$  g) at 0730 and 1930 hours with a digital balance. Every 3 days, we measured wing length ( $\pm 1$  mm) with a stopped wing rule and tarsus length ( $\pm 0.1$  mm) with callipers. We calculated an index of chick body condition (BC) at 1930 hours each evening relative to the mean mass for study chicks of each age ( $m_{\text{mean}}$ ), using the formula  $BC = m \times 100 / m_{\text{mean}}$ . Meal sizes are large relative to body mass, and the body condition index therefore largely reflects recent provisioning efforts. This index varied between 43 and 151 (mean = 100) and was independent of chick age (linear regression:  $P > 0.5$ ). Meal sizes and feeding frequencies were calculated from changes in chick body mass recorded overnight and corrected for mass lost through digestion, respiration and excretion between weighings (Quillfeldt et al. 2003). Briefly, we calculated weight loss before and after feeding events, in relation to the weight of the chick at the beginning of the interval. We first determined whether chicks had been fed, by using a regression equation from intervals before feeding (Quillfeldt et al. 2003). For the remaining chick nights on which feedings occurred, we calculated the daily mass loss by using the regression equation for the mass loss after feeding, starting with the evening weight. Meal sizes were calculated as the sum of the observed mass change overnight and the estimated metabolic mass loss.

### Experimental Manipulation

To test the relations between body condition, hormone levels and begging intensity, we carried out a cross-fostering experiment, starting on 24 February 2003, with five 'light' chicks (mean BC before 24 February 82–92) and five 'heavy' chicks (mean BC before 24 February 110–120). By exchanging chicks between nests we experimentally altered chick body condition to document effects on hormone levels and behaviour. Within pairs, chicks were matched for age (16–22 days). After pairwise exchange of the chicks between their nests, they were weighed twice daily, as for the control period (i.e. before 24 February), for 10 days. They remained in their foster nests after the study, and all 10 chicks fledged successfully. The remaining 10 chicks (mean BC 94–109) were used as controls, and were weighed daily as for the control period.

### Recordings of Begging Calls

We initially recorded begging in 24 nests, but later on could not reach chicks of two nests, as they went to deeper parts of their nest chambers, so the final sample size was 22 chicks. We recorded the vocal behaviour of chicks at each study nest overnight on 15 consecutive nights during the control period and 10 nights during the experimental period by placing a portable tape recorder outside the nest entrance and an external microphone with a 2-m connection in the nest entrance close to the nest chamber. The recorders were switched on at 2300 hours each night (before the first adults returned) and recorded at low speed until the end of the tape (about 95 min). Not all recordings contained begging sessions, so sample sizes ranged from one to eight successfully recorded sessions per nest and period. Because our recordings terminated before the adults left the burrows at the end of the night, we may have missed some late feedings. To compare all chick nights, we therefore included only the first begging sessions of each chick and night in the analyses of begging behaviour. Daily variation in begging behaviour therefore reflected the chick's need at the time of adult arrival. The terms 'rhythmic calls' and 'long begging calls' are used according to Quillfeldt (2002), where spectrograms for these call types are given for Wilson's storm petrels.

### Blood Sampling

Blood samples (200–300  $\mu\text{l}$ ) were collected from the brachial vein in heparinized capillaries immediately after capture (handling time 1–2 min), centrifuged and stored at  $-20^\circ\text{C}$  until later analysis. Chicks ( $N = 22$ ) were sampled at 9–36 days of age after capture by hand (mean interval = 5 days). In the experimental period, we took two to three samples from each chick. Most samples were taken in the daytime (0800–1100 hours), but we took seven samples at midnight to test for diurnal variation. The nocturnal hormone levels were not included in the calculations of the mean values of chicks. Additional blood samples for the analysis of testosterone and corresponding begging calls were taken in the 2003–2004 season ( $N = 36$  unmanipulated chicks) with the same methods as described for 2002–2003.

### Hormone Assays

We carried out hormone analysis by radioimmunoassay. Testosterone concentrations were measured in duplicate 20- $\mu\text{l}$  plasma samples by direct radioimmunoassay; we used antitestosterone antiserum (code 8680-6004, Biogenesis, Poole, U.K.) and [ $^{125}\text{I}$ ]-testosterone label (code 07-189126, ICN, Basingstoke, U.K.; Parkinson & Follett 1995). Interassay variation was 16.6% and intra-assay variation was 11.0%. The antiserum not only detects testosterone but also cross-reacts with other androgens present in the blood, although this cross-reactivity is low. Four solvent blanks were also included in each assay, and showed no testosterone. The mean 50% binding was

at 6.5 pg/tube for 20  $\mu$ l plasma and the mean detection limit was 0.035 ng/ml.

Corticosterone concentrations were measured after extraction of 20- $\mu$ l aliquots of plasma in diethyl ether, by radioimmunoassay (Wingfield et al. 1992); we used anticorticosterone antiserum (code B3-163, Esoterix Inc Endocrinology, San Diego, CA, U.S.A.) and [1,2,6,7-<sup>3</sup>H]-corticosterone label (Amersham, Little Chelfont, U.K.). The assay was run with 50% binding at 90 pg/tube and the extraction efficiency was 80–90%. The intra-assay variation was 4.1% and the detection limit (for 7.3- $\mu$ l aliquots of extracted plasma) was 0.4 ng/ml. Values below the detection limit (8/87 samples) were assigned values of 0.4 ng/ml.

### Data Analysis

For statistical tests we used SPSS 10.0 (SPSS Inc., Chicago, IL, U.S.A.). To avoid unreliable assessments of the effects of covariates (see below) we included in the analysis only those 10 chicks from which we had obtained recordings from at least 3 nights. Normality was tested with Kolmogorov–Smirnov tests. We used univariate analyses of covariance (ANCOVA) based on Type III sum of squares to test for the influences of body condition on calling and of calling on meal size. To control for individual differences between chicks and to avoid pseudoreplication (e.g. Quillfeldt 2002), we included chick as a categorical independent variable ('factor') in these analyses. We initially included the interaction between the factor chick and the covariate in the model, but removed it as it did not reveal significance (all  $P > 0.22$ ). In addition to the results of these analyses, we report tests of the call parameters to enable easier interpretation. To indicate the direction of the relation, we calculated Pearson correlations between the covariate and the response variable, separately for each subject. The average correlation coefficient between the response variable and the covariate indicates the degree and the direction of the relation between the two variables. As a measure of effect sizes we used partial eta-square values ( $\eta^2$ ; i.e. the proportion of the effect plus error variance that is attributable to the effect) in the case of variables and covariates tested with an ANCOVA. The sums of the partial eta-square values are not additive (e.g. [http://web.uccs.edu/lbecker/SPSS/glm\\_effectsize.htm](http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm)). When using a  $t$  test of correlation coefficients, we report the average coefficient of determination (correlation coefficient<sup>2</sup>) as a measure of effect size.

Means are given  $\pm$  SEs. When several tests of a single null hypothesis were carried out, we added alpha-level adjustments as follows. We corrected significant  $P$  values for the number of tests, applying the equation  $P_{\text{corr}} = 1 - (1 - \alpha)^k$ , which we derived from conversion of the Dunn–Šidák method (Sokal & Rohlf 1995). In this equation,  $P_{\text{corr}}$  denotes the corrected  $P$  value,  $\alpha'$  is the originally derived  $P$  value, and  $k$  is the number of tests.

For pairwise tests between daytime and midnight hormone levels, we used exact nonparametric tests as required for small samples (Siegel & Castellan 1988; Mundry & Fischer 1998).

### Ethical Note

We recorded chick calls without any detectable influence on the birds. The recorders were situated outside the nest burrows, and only a small microphone was placed in the nest. Chicks were weighed during the day, when nests were not attended by an adult, and no desertion occurred. The chicks were caught by hand and no regurgitation of stomach oil or food occurred. All handled chicks fledged normally. The New Island South Conservation Trust granted permission to work on the island, and all work was approved by the Falkland Islands Government (Environmental planning office).

## RESULTS

### Begging and Provisioning

Thin-billed prions used two types of calls. In response to the arrival of an adult, chicks first used rhythmic call series, which lasted for a few seconds up to 45 min, followed by long begging calls during feedings. Begging sessions lasted an average of  $12.2 \pm 0.5$  min (range 1–27 min), the number of calls per session averaged  $307.7 \pm 17.6$  (65–756), the mean call rate was  $24.7 \pm 0.7$  calls/min (9.3–37.6) and the maximum call rate that chicks sustained over 1 min was  $37.2 \pm 1.0$  calls/min (13–63). We found significant correlations between all combinations of call parameters except session duration and maximum call rate (Pearson correlation: number of calls versus duration:  $r_{18} = 0.904$ ,  $P < 0.001$ ; number of calls versus maximum call rate:  $r_{22} = 0.502$ ,  $P = 0.012$ ; number of call versus mean call rate:  $r_{22} = 0.824$ ,  $P < 0.001$ ; duration versus maximum call rate:  $r_{22} = 0.306$ ,  $P = 0.146$ ; duration versus mean call rate:  $r_{22} = 0.561$ ,  $P = 0.004$ ; maximum call rate versus mean call rate:  $r_{22} = 0.730$ ,  $P = 0.001$ ).

Variation in the body condition index of individual chicks over time was smaller than the variation between chicks (general linear model, GLM:  $F_{22,245} = 4.65$ ,  $P < 0.001$ ). We therefore analysed the data controlling for the effect of individual differences. When we controlled for body condition index, the total call number, maximum call rate and duration of begging sessions varied significantly between chicks ( $P < 0.002$ ; Table 1).

There was a strong relation between body condition index and parameters of begging intensity (Table 1). The total number of begging calls and the mean and maximum call rates were negatively related to the body condition index (Table 1), but session duration was not significantly correlated with body condition index (Table 1).

To assess between-chick effects of body condition index and begging, we calculated the mean body condition index and the means of the begging call parameters of chicks. The mean body condition index of chicks was negatively correlated with their mean call rate (Pearson correlation:  $r_{21} = -0.54$ ,  $P = 0.010$ ,  $P_{\text{corr}} = 0.039$ ; Fig. 1a). We found no correlation between mean body condition index and mean total number of calls per begging session ( $r_{21} = -0.28$ ,  $P = 0.213$ ), mean maximum rate ( $r_{21} = -0.36$ ,  $P = 0.097$ ) or mean begging session duration ( $r_{21} = 0.10$ ,  $P = 0.672$ ).

**Table 1.** Within-chick effect of body condition index on call parameters

Response variable	$F_{1,9}$	$P$	$P_{corr}$	Effect size ( $\eta^2$ )	Average rho
Session duration (min)	2.24	0.144	0.463	0.063	-0.08
Total call number	7.11	<b>0.011</b>	<b>0.043</b>	0.177	-0.34
Mean call rate (calls/min)	7.42	<b>0.010</b>	<b>0.039</b>	0.184	-0.33
Maximum call rate (calls/min)	10.80	<b>0.002</b>	<b>0.008</b>	0.247	-0.30

The relation between the body condition index (covariate) and parameters of begging (response variables) was tested with an ANCOVA, including chick as a factor. Significant  $P$  values are marked bold. Average rho indicates average Pearson correlation coefficients between the covariate and body condition index, calculated for each chick separately;  $P_{corr}$  indicates  $P$  values corrected for the number of tests (four); effect sizes denote partial eta-squares ( $\eta^2$ ).

Since adults may respond to differences in begging intensity immediately (regurgitating more or less food) or later (regulating feeding frequency or meal size), we used ANCOVA to test for effects of begging calls on meal sizes. When chicks uttered more begging calls and calls at a higher rate, they received more food (Table 2). The duration of begging call sessions was not correlated with the size of the meal.

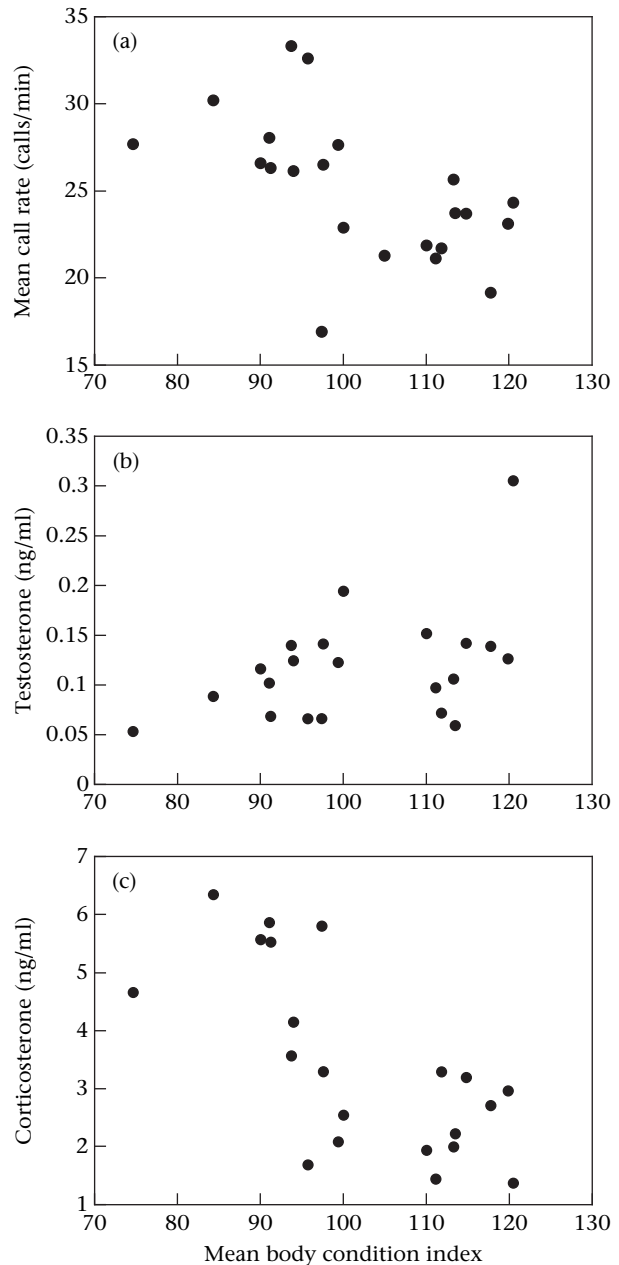
### Hormone Production

There was significantly more variation between than within chicks for multiple samples from the same individual chicks for testosterone but not for corticosterone (ANOVA, chicks with at least four hormone samples included: testosterone:  $F_{7,35} = 5.99$ ,  $P < 0.001$ ; corticosterone:  $F_{7,32} = 1.25$ ,  $P = 0.313$ ). Neither testosterone nor corticosterone varied with chick age within our sample (GLM, effect of age within chicks: testosterone:  $F_{1,63} = 0.84$ ,  $P = 0.366$ ; corticosterone:  $F_{1,63} = 0.39$ ,  $P = 0.534$ ).

Between chicks, there was a significant correlation between a chick's mean body condition index and its mean hormone levels (Fig. 1b, c). The correlation with body condition index was positive for testosterone (Pearson correlation:  $r_{20} = 0.47$ ,  $P = 0.031$ ), but negative for corticosterone ( $r_{20} = -0.709$ ,  $P < 0.001$ ). There were no such effects within chicks. The mean values for each chick of corticosterone and testosterone were negatively correlated ( $r_{20} = -0.41$ ,  $P = 0.022$ ).

During the control period, mean testosterone of individual chicks was significantly and positively correlated with two measures of begging intensity (mean data for each chick are included, both years combined; Pearson correlation: maximum call rate:  $r_{56} = 0.32$ ,  $P = 0.007$ ,  $P_{corr} = 0.021$ ; mean call rate:  $r_{56} = 0.33$ ,  $P = 0.006$ ,  $P_{corr} = 0.018$ ; total call number:  $r_{56} = 0.26$ ,  $P = 0.024$ ,  $P_{corr} = 0.07$ ; Fig. 2).

When we used only data from the 2002–2003 season, mean testosterone and corticosterone levels of individual



**Figure 1.** Correlation between the mean body condition index of thin-billed prion chicks and (a) their mean call rate during begging, (b) their mean testosterone levels and (c) their mean corticosterone levels.

chicks were not correlated with measures of begging intensity (all correlations between testosterone or corticosterone and total call number, duration, maximum call rate and mean call rate:  $P > 0.15$ ), but the sample size was relatively small ( $N = 21$ ). When we considered the 2003–2004 season alone, mean testosterone of individual chicks was significantly correlated with two measures of begging rate (Pearson correlation: maximum call rate:  $r_{35} = 0.34$ ,  $P = 0.04$ ,  $P_{corr} = 0.115$ ; mean call rate:  $r_{37} = 0.35$ ,  $P = 0.006$ ,  $P_{corr} = 0.018$ ; total call number:  $r_{35} = 0.25$ ,  $P = 0.135$ ).

Corticosterone was higher at midnight ( $12.1 \pm 5.4$  ng/ml) than during the day ( $3.33$  ng/ml); (exact Wilcoxon

**Table 2.** Within-chick effects of call parameters on meal size on the night of recording

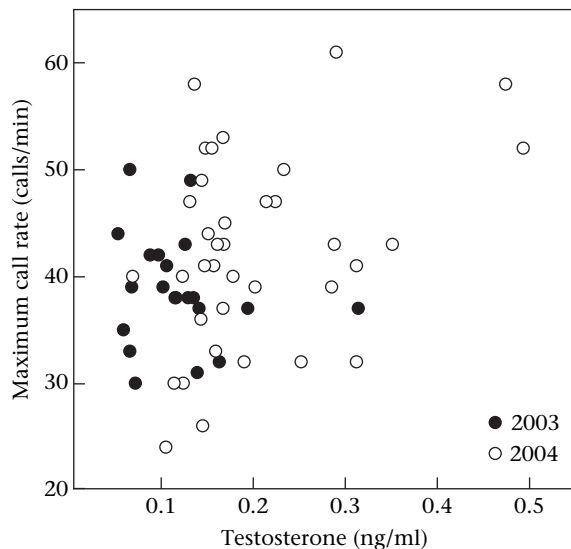
Covariate	$F_{1,9}$	$P$	$P_{corr}$	Effect size ( $\eta^2$ )	Average rho
Session duration (min)	0.26	0.611	0.977	0.008	0.20
Total call number	7.52	<b>0.010</b>	<b>0.039</b>	0.186	0.39
Mean call rate (calls/min)	10.22	<b>0.003</b>	<b>0.012</b>	0.237	0.43
Maximum call rate (calls/min)	4.94	<b>0.033</b>	0.126	0.130	0.30

The relation between the meal size (response variable) and a parameter (covariate) was tested with an ANCOVA, including chick as a factor. Significant  $P$  values are marked bold. Average rho indicates average Pearson correlation coefficients between the covariate and meal size, calculated for each chick separately;  $P_{corr}$  indicates  $P$  values corrected for the number of tests (four); effect sizes denote partial eta-squares ( $\eta^2$ ).

signed-ranks test, mean corticosterone in the daytime versus at midnight:  $T^+ = 27$ ,  $N = 7$  chicks,  $P = 0.031$ ). In contrast, the testosterone values remained unchanged at midnight, averaging  $0.144 \pm 0.020$  ng/ml (mean daytime versus midnight:  $T^+ = 15$ ,  $N = 7$  chicks,  $P = 0.938$ ).

### Cross-fostering Experiment

During the experimental period, the significant difference in body condition index between control, light experimental and heavy experimental chicks disappeared (Table 3). Light chicks transferred to the nests of heavy chicks gained 6% in their body condition index, on average, whereas heavy chicks transferred to the nests of light chicks lost an average of 8%. The difference in body condition index change between light and heavy chicks

**Figure 2.** Correlation between maximum call rate during begging and testosterone production of thin-billed prion chicks in two breeding seasons.

was statistically significant (independent samples  $t$  test:  $t_8 = -2.5$ ,  $P = 0.04$ ).

During the control period, chicks of the heavy group had the highest mean feeding rates, followed by control chicks, and light chicks had the lowest (Fig. 3). During the experimental period, both experimental groups were fed more than the control chicks, with the initially light chicks achieving the highest increase in feeding rates (Fig. 3).

During the experimental period, the initial difference between chicks in corticosterone secretion during the control period changed; the corticosterone levels of initially light chicks declined to about one-third of the initial level (Table 3). Heavy chicks increased their corticosterone levels after being placed in foster nests, and thus were statistically indistinguishable from controls (Table 3). The change in corticosterone induced by cross-fostering was correlated with the change in body condition index (Pearson correlation:  $r_8 = 0.983$ ,  $P < 0.001$ ; Fig. 4).

During the control period, light chicks had low testosterone levels, whereas heavy chicks did not differ in their testosterone levels from controls (Table 3). Control chicks showed no differences in testosterone levels between control and experimental periods, whereas experimental chicks increased their testosterone levels during cross-fostering (pairwise  $t$  test: controls:  $t_9 = 1.5$ ,  $P = 0.185$ ; cross-fostered chicks:  $t_8 = 3.9$ ,  $P = 0.004$ ). Cross-fostering led to higher testosterone levels during the experimental period in initially heavy chicks than in initially light chicks ( $t_8 = 2.5$ ,  $P = 0.038$ ; Table 3).

Mean call rates and numbers of calls during the control period did not differ between light and control chicks, whereas heavy chicks had lower call rates (Table 3). Initially light chicks and control chicks did not change their begging behaviour during the experiment. Although most heavy chicks placed in foster nests increased their call rates and uttered about twice as many calls per feeding session as during the control period, differences were not significant ( $P = 0.052$ ,  $P_{corr} = 0.101$ ; Table 3). The increase in call number in experimental chicks was correlated with the increase in both corticosterone and testosterone (Spearman correlation: corticosterone:  $r_5 = 0.783$ ,  $N = 9$ ,  $P = 0.013$ ; testosterone:  $r_5 = 0.7333$ ,  $N = 9$ ,  $P = 0.025$ ; Fig. 5).

### DISCUSSION

In this study, we tested the hypotheses that (1) chicks honestly signal their nutritional state to their parents and parents respond to begging by delivering larger meals and (2) chick androgens and corticosterone covary with begging behaviour. Our results are in agreement with both hypotheses. Begging increased with decreased body condition index within and between chicks, and the mean chick body condition index correlated positively with testosterone levels and negatively with corticosterone levels. Between chicks, the mean testosterone of individual chicks was correlated positively with measures of their begging intensity. Adults responded to more intense begging by delivering larger meals. Furthermore, chicks that had increased testosterone and corticosterone

**Table 3.** Body condition index, steroid hormone secretion and parameters of begging calls ( $\bar{X} \pm SE$ ) of thin-billed prion chicks in response to a cross-fostering experiment

Parameter	Chicks			ANOVA		Tukey test					
	Control (N=10)	Heavy (N=5)	Light (N=5)	$F_{2,19}$	P	Light versus heavy		Heavy versus control		Light versus control	
						q	P	q	P	q	P
<b>Body condition index</b>											
Control period	99.4±2.2	112.1±2.1	88.8±2.5	17.9	<0.001	8.4	<0.001	5.3	0.004	4.4	0.016
Experimental period	99.9±3.1	104.5±4.2	94.7±4.1	1.3	0.298						
Difference	0.5±2.5	-7.6±4.8	5.9±2.7	3.4	0.058						
<b>Mean corticosterone (ng/ml)</b>											
Control period	3.8±0.5	2.1±0.3	5.6±0.3	10.0	0.001	6.3	0.001	3.5	0.056	3.8	0.042
Experimental period	2.3±0.5	3.0±1.2	1.8±0.4	0.6	0.576						
Difference	-1.7±0.7	1.3±1.4	-3.8±0.6	6.2	0.009	4.9	0.008	3.4	0.072	2.4	0.248
<b>Mean testosterone (ng/ml)</b>											
Control period	0.114±0.012	0.112±0.020	0.080±0.012	1.5	0.253						
Experimental period	0.137±0.012	0.176±0.011	0.120±0.020	3.1	0.073						
Difference	0.016±0.011	0.067±0.017	0.040±0.012	3.8	0.042	1.8	0.437	3.9	0.035	1.8	0.419
<b>Mean call rate (calls/min)</b>											
Control period	26.7±1.2	22.8±1.2	26.5±2.7	1.5	0.242						
Experimental period	25.3±1.7	28.1±2.4	24.9±3.8	0.4	0.664						
Difference	-2.4±1.4	5.3±3.4	-1.6±3.8	2.6	0.107						
<b>Total number of calls</b>											
Control period	327.1±28.0	276.5±40.0	367.9±53.6	1.1	0.351						
Experimental period	336.5±33.3	537.4±111.3	357.9±86.4	2.4	0.118						
Difference	9.4±31.1	260.9±126.3	-10.0±99.7	3.5	0.052						

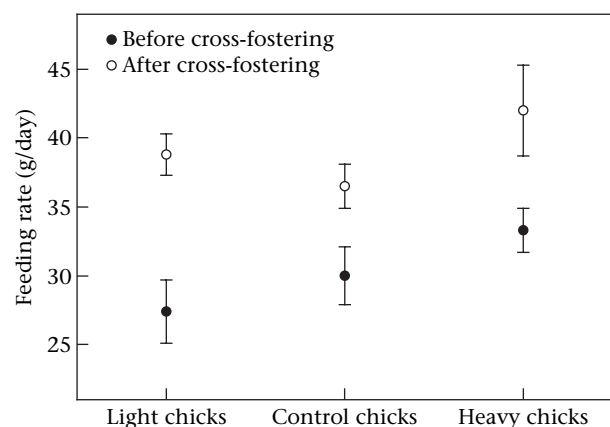
The chicks of the heavy group were fostered in nests of initially light chicks and vice versa. For each parameter (body condition, hormones and two measures of begging calls), the mean during the control and experimental periods is given, as well as the difference between the control period and the experimental period. One chick of the heavy experimental group was not blood sampled before cross-fostering, so the sample size for hormone samples is 4.

after being placed in a foster nest also increased their begging. Although we did not manipulate hormone levels, this is the first study to document correlations between experimentally induced changes in concentrations of endogenous hormones and begging behaviour in nestling birds. These results open the possibility that the intensity of chick begging is under hormonal control and forms a mechanism controlling parental provisioning in procelariiform seabirds. We suggest that chick behaviour can explain much of the variation in growth patterns between individual birds.

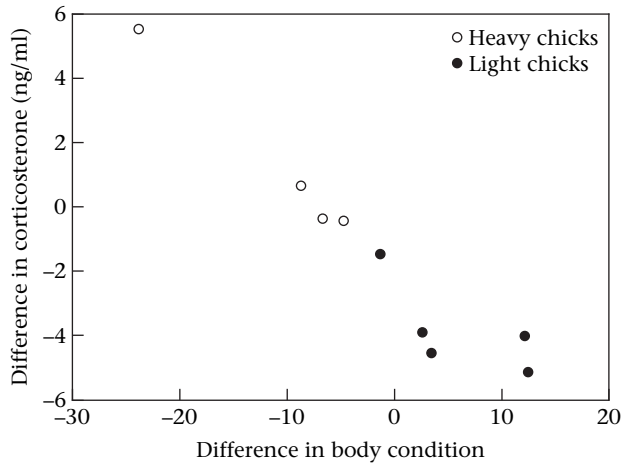
### Hormones and the Regulation of Begging

The only previous studies to include the analysis of hormones and begging in birds, to our knowledge, focused on maternal testosterone (Schwabl 1996; Eising & Groothuis 2003) and effects of implanted corticosterone (Kitaysky et al. 1999, 2001a, b, 2003). In our study, cross-fostered chicks adjusted their hormone levels and begging rates. The differences in both corticosterone and testosterone levels were positively correlated with measures of begging intensity, suggesting that both hormones are involved in the regulation of begging. The main hormonal effects were a decrease in corticosterone in initially light chicks and a strong increase in testosterone in initially heavy chicks, when they were faced with lower delivery

rates. Most initially heavy chicks, which had a 50% increase in testosterone, altered their begging call intensity. On average, they increased their begging efforts twofold after being placed in foster nests with initially poor provisioning rates, but their corticosterone levels were not



**Figure 3.** Feeding rates ( $\bar{X} \pm SE$ ) for control and experimental thin-billed prion chicks in a cross-fostering experiment. In the control period, before cross-fostering, all chicks were fed in their own nests; in the experimental period, after cross-fostering, five pairs of initially heavy and light chicks were fed in each other's nests. Control chicks remained in their original nests.



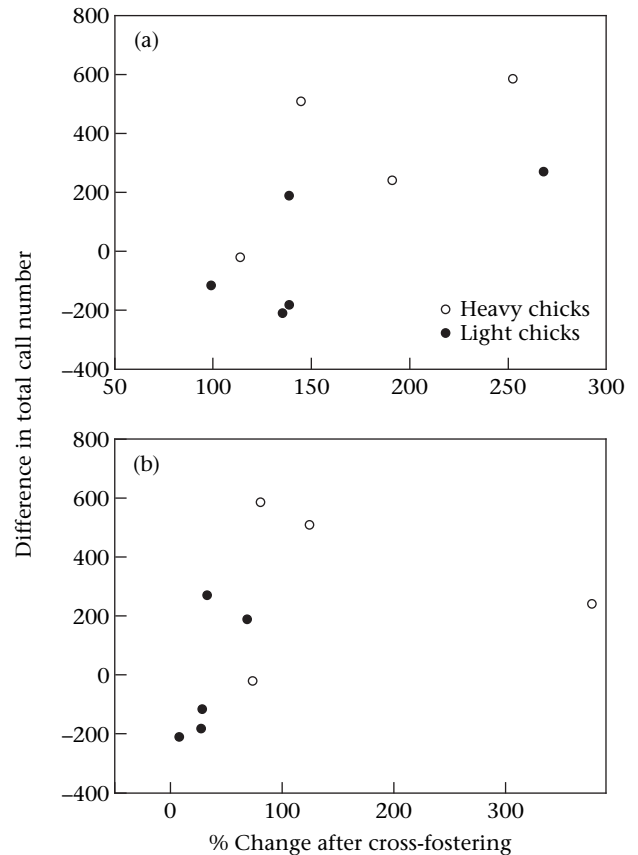
**Figure 4.** Relation between the change in body condition index during the cross-fostering experiment between control and experimental periods and the change in corticosterone of experimental chicks measured during control and experimental periods.

statistically different from those of controls. Therefore, endogenously produced testosterone was more strongly related to begging than corticosterone.

This conclusion is further supported by evidence from the initially light chicks. Before the cross-fostering started, light chicks did not have higher rates or numbers of begging calls than controls, despite having higher corticosterone levels. Furthermore, initially light chicks did not change their begging behaviour during the experiment, although their corticosterone levels decreased to one-third of those during the control period.

The base levels and dynamics of steroid hormones of seabird chicks have not been well studied. The baseline levels of corticosterone found in the present study were in the same range as in chicks of other seabird species (Wilson's storm petrel: Quillfeldt et al. 2004b; red-legged kittiwake, *Rissa brevirostris*: Kitaysky et al. 2001b; black-legged kittiwake: Kitaysky et al. 1999; blue-footed booby, *Sula nebouxi*: Nuñez de la Mora et al. 1996). An increase in baseline corticosterone levels in response to food deprivation of days to weeks has been shown experimentally in the latter three species. In contrast, 3–4-month-old king penguins, *Aptenodytes patagonica*, can tolerate the major part of the natural winter fast (about 100 days) without a substantial increase in corticosterone secretion, increasing corticosterone only towards the end of the fast of 4–6 months (Le Ninan et al. 1988). Testosterone was undetectable (below 0.06 ng/ml) in 15–20-day-old chicks of the blue-footed booby, but was found in a similar range to the present values in black-legged kittiwakes (Kitaysky et al. 1999).

We were also interested in diurnal patterns of hormones in chicks of thin-billed prions, which are fed during the night. Corticosterone was higher at midnight than in the daytime, whereas testosterone remained unchanged. This pattern of corticosterone is in contrast to that in diurnal bird species, where basal plasma corticosterone levels peak in the early morning, before the active period begins ('pre-active peak', Breuner et al. 1999; Romero & Remage-Healey 2000; Tarlow et al. 2003). Corticosterone is



**Figure 5.** Relation between the difference in hormone secretion between control and experimental periods and the difference in the total number of begging calls during feeding sessions of experimental chicks during the cross-fostering experiment. (a) Testosterone; (b) corticosterone.

involved in the regulation of energy utilization, and corticosterone rhythms are often associated with activity and foraging patterns. The presumed function of the pre-active peak is to prepare the body for the energy-demanding active period (e.g. Breuner et al. 1999). Similarly, the high midnight corticosterone levels found in the present study may be related to the nocturnal feeding regime.

### Regulation of Provisioning

Chicks of pelagic seabirds may accumulate large lipid reserves, attaining peak masses of nearly twice that of their parents partway through the growth period. This nestling obesity has stimulated much discussion, because parents seem to be provisioning at rates much higher than necessary for successful fledging. At the end of nestling development, chicks lose mass until they are almost at adult mass. However, there are large differences between individuals, between colonies and between breeding seasons. The analysis of these differences under natural and experimental situations may lead us to understand better the adaptive function of nestling obesity in pelagic seabirds.

The initial difference in body condition index between heavy and light chicks (24%) was reduced to 10% during



the 10-day experimental period. Both experimental groups were fed more than control chicks (Fig. 3), but possibly for different reasons. In initially light chicks, there was no change in begging, indicating that the increase in feeding rate and 6% increase in body condition index were due to the higher delivery rates of the foster parents than to the natural parents.

In contrast, heavy chicks increased their begging call rates twofold and although they lost 8% of their initial body condition, they had the highest feeding rates of all groups. This difference means that parents with the poorest initial provisioning rates were stimulated by chick begging to deliver the highest feeding rates. The results also indicate that heavy chicks could afford the cost (assuming that begging is costly) of increased begging, but light ones could not. Thus, the increase in delivery rates was controlled by the behaviour of the chicks. This result is in line with results of brood manipulation experiments of passerines, in which parents increased their provisioning rates in response to increased brood sizes (e.g. Wright & Cuthill 1990), suggesting that this adaptive parental response occurs in relation to signals indicating the value of the reproductive attempt. However, the natural parents of the heavy chicks delivered at high rates to the cross-fostered light chicks even though the chicks had normal to low begging rates.

In altricial birds, parental care consists of supplying divisible resources to dependent young, whereby the optimal level of investment in any reproductive attempt is higher for the offspring than for their parents, promoting the evolution of parent–offspring conflict (Trivers 1974). The existence of parent–offspring conflict influences the patterns of growth and development of young birds in the nest, and may favour the evolution of specialized signalling systems. An offspring will have better knowledge of its real need than will its parents, and it would therefore benefit both offspring and parents if parents respond to cues that signal need. However, once such a system has evolved, the offspring can exploit it to gain more food than the parent is selected to give (Trivers 1974). Parental body condition is also variable, and chicks must be sensitive to such variation and must adjust their behaviour appropriately, as low investment by a parent in poor condition differs from low investment by a parent in good condition (Trivers 1974).

In our cross-fostering experiment, we found evidence of behavioural adjustment, as predicted by parent–offspring conflict. In particular, poorly provisioning parents did not invest at the maximum possible rate, and they increased provisioning as the apparent need of the chicks increased. Furthermore, heavy chicks did not beg at the maximum rate in their original nests, but increased begging only in the foster nests.

Evolutionary theory predicts that parents should avoid investing in unrelated young (Hepper 1986) and invest only in their own offspring or kin (Beecher et al. 1985). However, parents need not recognize their offspring to avoid misdirecting parental care. In nidicolous birds, contact between young and parents may be maintained before fledging simply by strong nest site attachment (Redondo 1993). Chicks and adults of procellariiform

seabirds can identify their own nests by smell (Minguez 1997; Bonadonna et al. 2004), and adults use smell to return to their burrows and to find their chicks. In the cross-fostering experiment in our study, adults were thus probably unaware that they were feeding unrelated chicks and invested as heavily as demanded by the chick. Chicks, on the other hand, were placed in burrows that had an unfamiliar smell. It is therefore possible that the cross-fostered heavy chicks begged more because they were exploiting unrelated parents, and did not need to be sensitive to the adults' body condition.

Studies of begging in other procellariiform seabirds (Quillfeldt 2002; Quillfeldt et al. 2004a; Quillfeldt & Masello 2004) have also highlighted individual differences in chick calling behaviour. After controlling for the effect of body condition, we found that chicks still varied in their calling behaviour. Models for the resolution of the parent–offspring conflict have assumed genetic variation for levels of offspring solicitation, to allow offspring and parental strategies to coevolve and the conflict to be evolutionarily resolved, and there is evidence from a variety of animals that such variation exists (Agrawala et al. 2001; Kölliker & Richner 2001). Further studies are needed on the origins of the hormonal and behavioural differences between individuals, their possible heritability, the influence of environmental variability and the costs incurred through such mechanisms which might explain hormonal control of begging and signal honesty.

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