

Begging and provisioning of Thin-billed prions *Pachyptila belcheri* is related to testosterone and corticosterone

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Running title: Begging and hormones of Thin-billed prions

Abstract

1. Vigorous begging is usually seen as an expression of parent-offspring conflict over limited resources. Chicks signal their 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, the costs of the signal may be coupled to the expression of such hormones, if they are closely associated with the signal.
2. We tested whether begging in chicks of Thin-billed prions *Pachyptila belcheri* (Procellariiformes, Aves) is associated with secretion of corticosterone and testosterone by the chicks.
3. Prion chicks honestly signalled their nutritional state to their parents. Begging increased with decreased body condition, both within and between chicks. Adults responded to more intense begging by delivering increased meal sizes.
4. We found evidence that corticosterone and testosterone secretion play a major role in this signalling system. The mean body condition of chicks correlated positively with testosterone levels and negatively with corticosterone levels and in a cross-fostering experiment, the change in testosterone and corticosterone between the control period and the experimental period was positively correlated with the change in begging intensity.
5. This is the first direct experimental test suggesting that the control of chick begging by endogenously produced testosterone and corticosterone forms a mechanism controlling parental provisioning in birds and that chick behaviour can explain part of the variation in growth patterns observed between individual birds.

Keywords: endocrine control of signalling, Falkland Islands, honest signalling, parent-offspring conflict, Procellariiformes

Introduction

Avian nestlings commonly beg to obtain food from their parents. Begging in birds is used as a model to study parent-offspring conflict and the evolution of signalling (Wright & Leonard 2002, Mock & Parker 1997). Vigorous begging is usually seen as an expression of conflict over resource allocation between parents and offspring. Nestlings beg using vocal signals, gape colour and postural displays to transfer information about their nutritional state and health (Kilner 1997, Wright & Leonard 2002). The conflicting interests between parents and offspring about the distribution of limited resources might lead to dishonest exaggeration of begging signals unless they are reigned in by costs (Godfray 1995; Rodriguez-Gironés 1999). A number of possible costs have been identified (reviewed by 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 (Platzen & Magrath 2004). However, according to the present evidence, the mechanisms underlying these observed effects remain to be identified. Because hormones associated with stress and hunger (corticosterone) and aggressive behaviour (testosterone) have deleterious effects, the costs of the signal may also be coupled to endocrine control, if these are associated with the signal.

Most studies of begging have been carried out in passeriform birds, where nestlings are raised in the competitive environment of broods containing several individuals. This may pose a problem to 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 in the absence of scramble competition.

Pelagic seabirds of the Order Procellariiformes provision their chicks infrequently compared to other birds. The chicks accumulate large lipid reserves, attaining peak masses of up to 190% of adult mass. At the end of nestling development, chicks lose mass and fledge close to adult mass. The extreme patterns of provisioning and growth of pelagic seabirds have attracted considerable discussion, the main question is: How are provisioning rates regulated, and what explains the large differences between individual offspring? Nearly all previous studies suffer from a lack of analyses of parent-offspring interactions, and could therefore not adequately account for the influence of chick behaviour. However, several authors suggested that chicks often reject food and thus may have considerable influence on provisioning.

The only avian order with an obligate clutch size of one is 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 transferred meal sizes in Wilson's storm-petrels (Quillfeldt 2002), Manx shearwaters (Quillfeldt *et al.* *In Press*) and Cory's shearwaters (Quillfeldt & Masello *unpubl. data*). Furthermore, in Wilson's storm-petrels, chicks with a low body condition have increased levels of corticosterone, a hormone which may stimulate begging behaviour (Quillfeldt & Möstl 2003). Thus, the secretion of corticosterone might provide a mechanistic link between the physiological condition and behavioural interactions among adults and their young. Individual differences in hormone secretion or receptivity may account for individual differences of begging behaviour and growth.

In the present study, we analysed hormonal regulation of chick behaviour in parent-offspring interactions in Thin-billed prions, *Pachyptila belcheri*. Specifically, to test the following hypotheses:

- 1) Chicks honestly signal their nutritional state to their parents and parents respond to begging by delivering larger meals.
- 2) Chick androgens and corticosterone control begging behaviour.

Materials and methods

The study was carried out in on New Island, Falkland Islands, from 8 January to 4 February 2003. Thin-billed prions breed in the Falkland Islands, Isla Noir (Chile), Crozet and Kerguelen. New Island is the most important known breeding site for Thin-billed prions. Up to 2 million pairs bred on this island in 2001/2002 (Catry *et al.* 2003).

Thin-billed prions 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 low disturbance to the birds. The life cycle and basic biology of Thin-billed prions have been described by Strange (1980), and data of the breeding season 2002/2003 were analysed (Quillfeldt *et al.* 2003). Further studies of the biology of Thin-billed prions were carried out in Kerguelen, including studies of sexual dimorphism of voice and morphology (Genevois & Bretagnolle 1995), feeding ecology (Cherel *et al.* 2002; Chastel & Bried 1996) and parental investment (Duriez *et al.* 2000; Weimerskirch *et al.* 1995).

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). Thin-billed prions are burrow nesters, and nests were accessed via short access tunnels in the roof of each burrow, capped with removable stone lids. This system facilitated rapid access to chicks, reducing overall disturbance. Nests were marked three years previously to the present season and monitored for eggs and hatching chicks.

If chicks were present on our first visit, we determined the hatching dates of chicks (to the nearest day) by calibrating wing length against wing growth in chicks of known age. Chicks were weighed daily at 07:30 and 19:30 hours to the nearest 1g using a digital balance. Wing length was measured every three days to the nearest 1 mm with a stopped wing rule. Tarsus length was measured every three days to the nearest 0.1 mm using callipers. An index of chick body condition at 1930 each evening was calculated relative to the mean mass for study chicks of each age (m_{mean}), using the following formula: $BC = m \cdot 100 / m_{\text{mean}}$. Meal sizes are large compared to the body mass, and body condition therefore largely reflects recent provisioning efforts. This index varied between 43 and 151 (with a mean value of 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, using equations in Quillfeldt et al. (2003) to correct for mass lost through digestion, respiration and excretion between weighings.

We carried out a cross-fostering experiment with five light chicks and five heavy chicks. Within pairs, chicks were matched for age (16-22 days). After pairwise exchange of the chicks between their nests on 24 February 2003, they were weighed twice daily as for the control period, for an experimental period of 10 days. They remained in their foster nests after the end of the study, and all 10 chicks fledged successfully. The remaining chicks were used as controls, and weighed daily, as for the control period.

Begging was recorded in 24 nests initially, but chicks of four nests could not be reached later as they went to deeper parts of their nest chambers, resulting in a final sample size of $n=20$ chicks. The vocal behaviour of nestlings at each of the study nests was recorded 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 2m 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 (*ca.* 95 min). Because not all recordings contained begging sessions, sample sizes ranged between one and 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. In order to compare all chick nights, we therefore included only first begging sessions of each chick and night in the analyses of begging behaviour. This way, daily variation in begging behaviour 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 samples (200-300 μ l) were collected from the brachial vein in heparinised capillaries immediately after capture (handling time 1-2 min), centrifuged and stored at -20°C until later analysis. Nestlings ($n = 22$) were sampled at 9-36 days of age after capture by hand, at a mean interval of 5 days. In the experimental period, 2 to 3 samples of each chick were taken. Most samples were taken at daytime (0800 to 1100 hours), while seven samples were taken at midnight to test for diurnal variation. The hormone levels measured at night were not included in the calculations of the mean values of chicks. Hormone analysis was carried out by radioimmunoassay (RIA). Testosterone concentrations were measured in duplicate 20 μ l plasma samples by direct radioimmunoassay, using anti-testosterone antiserum (code 8680-6004, Biogenesis, U.K.) and [^{125}I]-testosterone label (code 07-189126, ICN, U.K.) (Parkinson and Follett 1995). Inter-assay variation was 16.6% and intra-assay variation was 11.0%. A total of 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 μ l plasma and the mean detection limit was 0.035 ng/ml.

Corticosterone concentrations were measured after extraction of 20µl aliquots of plasma in diethyl ether, by radioimmunoassay (Wingfield, *et al.* 1992) using anti-corticosterone antiserum (code B3-163, Esoterix Inc Endocrinology, CA) and [1,2,6,7-3H]-corticosterone label (Amersham, U.K.). The assay was run with 50% binding at 90 pg/tube and the extraction efficiency was 80-90%. The intra-assay CV 4.1% and the detection limit (for 7.3µl aliquots of extracted plasma) was 0.4 ng/ml. Values below the detection limit (8/87 samples) were assigned values of 0.4ng/ml.

Statistical tests were performed in SPSS 10.0. Normality was tested with Kolmogorov-Smirnov tests. We used General Linear Models (GLIM) in order to control for individual differences in begging intensities between chicks and in order to avoid pseudoreplication (e.g. Quillfeldt 2002), including nest as a random factor and the test variables as covariates. In order to indicate the direction (positive or negative) of the correlation to the covariable, we included t values, and as a measure of effect sizes we included partial Eta-Squared-Values (η^2) in the tables (i.e. the proportion of the effect + error variance that is attributable to the effect). The sums of the partial Eta squared values are not additive (e.g. http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm). Means are given with standard errors.

Results

Begging and Provisioning

Feeding sessions were initiated by rhythmic calling, which lasted for a few seconds up to 45 minutes, followed by long begging calls during feedings (Tab.1).

Variation in the body condition of individual chicks over time was small compared to the variation between chicks (GLIM: $F_{22,245} = 4.65$, $P < 0.001$). The data were therefore analysed controlling for the effect of individual differences. Controlling for body condition, the call number, maximum call rate as well as the duration of begging sessions for a given body condition varied significantly between chicks (Tab. 2).

There was a strong relationship between chick body condition and parameters of begging intensity (Tab. 2). The total number of begging calls and the call rate both increased highly significantly with lower body condition (Tab. 2), while the maximum rate had a weaker relationship, and the duration was not statistically significantly correlated with the body condition (Tab. 2).

To assess between-chick effects of body condition and begging, we calculated the mean body condition and the means of begging parameters of chicks. The mean body condition of chicks was negatively correlated with their mean call rate ($r = -0.54$, $N = 22$, $P = 0.010$). We found no correlation between the mean body condition of chicks and their mean total number of calls per begging session ($r = -0.28$, $N = 22$, $P = 0.213$), their mean maximal rate ($r = -0.36$, $N = 22$, $P = 0.097$) or the mean begging session duration ($r = 0.10$, $N = 22$, $P = 0.672$).

Adults may respond to differences in begging intensity immediately (regurgitating more or less food) or later (regulating feeding frequency or meal size). We used GLIM to test for effects of begging calls on meal sizes (Tab. 3). When chicks uttered more begging calls and calls at a higher overall and maximum rate, they received more food (Tab. 3). The duration of begging call sessions was not correlated with the size of the delivered meal (Tab. 3).

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, for testosterone: $F_{7,35} = 5.99$, $P < 0.001$, for corticosterone: $F_{7,32} = 1.25$, $P = 0.313$). Between chicks, there was a statistically significant correlation of the mean body condition of a chick and its mean hormone levels. The correlation with body condition was positive for testosterone ($r = 0.47$, $N = 21$, $P = 0.031$), but

negative for corticosterone ($r=-0.709$, $N=21$, $P<0.001$). There were no such effects within chicks. The mean values for each chick of corticosterone and testosterone were negatively correlated ($r=-0.41$, $N=21$, $P=0.022$).

During the control period, mean testosterone and corticosterone levels of individual chicks were not correlated with measures of begging intensity, (all correlations between testosterone or corticosterone and total begging call number, begging duration, maximal begging rate and mean begging rate: $P>0.3$).

When we compared daytime and midnight hormone levels, corticosterone was elevated at midnight and averaged 12.1 ± 5.4 ng/ml (Wilcoxon Signed Ranks Test, mean daytime cort vs. midnight cort, $n=7$ chicks, $Z=2.20$, $P=0.028$). In contrast, the testosterone values remained unchanged at midnight, averaging 0.144 ± 0.020 ng/ml (Wilcoxon Signed Ranks Test, mean daytime T vs. midnight T, $n=7$ chicks, $Z=0.17$, $P=0.866$).

The cross-fostering experiment

During the course of the experimental period the significant difference in body condition between control, light experimental, heavy experimental chicks disappeared (Tab. 4). Light chicks switched into the nests of heavy chicks gained 6% body condition, on average, while heavy chicks switched into the nests of light chicks lost a mean 8%. The difference in body condition change between light and heavy chicks was statistically significant ($t = -2.5$, d.f. 8, $P = 0.040$).

During the control period, chicks of the heavy group had the highest mean feeding rates, followed by control chicks, while light chicks had the lowest mean feeding rates (Fig.1). 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.1).

The initial difference between chicks in corticosterone secretion during the control period changed during the experimental period, with the corticosterone levels of initially light chicks reduced to about one third of the initial level (Tab. 4). Heavy chicks increased their corticosterone levels after being placed in foster nests, and as a result were also statistically indistinguishable from controls during the experimental period (Tab. 4). The change in corticosterone induced by cross-fostering was correlated to the change in body condition (Fig. 2, $r=0.983$, $N=9$, $P<0.001$).

Light chicks had low testosterone levels during the control period, while heavy chicks did not differ in their testosterone levels from controls during the control period (Tab. 4). Control chicks did not show differences in testosterone levels between the control and experimental period, while experimental chicks increased their testosterone levels during cross-fostering (pairwise t-test for controls: $t = 1.5$, d.f. 9, $P = 0.185$; pairwise t-test for cross-fostered chicks: $t = 3.9$, d.f. 8, $P = 0.004$). Cross-fostering led to higher testosterone levels during the experimental period in initially heavy chicks than in light chicks (Tab. 4, light vs. heavy chicks: $t = 2.5$, d.f. 8, $P = 0.038$).

Begging rates and begging call numbers during the control period did not differ between light and control chicks, while heavy chicks had lower begging call rates (Tab. 4). Initially light chicks and control chicks did not change their begging behaviour during the experiment. In contrast, heavy chicks increased their begging efforts after being placed in foster nests by increasing begging rates and uttering about twice the number of begging calls per feeding session than during the control period (Tab. 4). The increase in begging call number in experimental chicks was correlated to the increase in both corticosterone and testosterone (Fig. 3; corticosterone: $r=0.783$, $N=9$, $P=0.013$; testosterone: $r=0.733$, $N=9$, $P=0.025$).

Discussion

Parent –offspring conflict arises because offspring attempt to solicit more resources than their parents should provide (Trivers 1974). In the present study, we analysed hormonal regulation of chick behaviour in parent-offspring interactions in Thin-billed prions, *Pachyptila belcheri*. Specifically, we were interested in testing the following hypotheses: 1. Chicks honestly signal

their nutritional state to their parents and parents respond to begging by delivering larger meals. 2. Chick androgens and corticosterone mediate begging behaviour.

Our results are in agreement with both hypotheses. Begging increased with decreased body condition within and between chicks, and the mean chick body condition correlated positively with testosterone levels and negatively with corticosterone levels. Adults responded to more intense begging by delivering increased meal sizes. Moreover, chicks which increased testosterone and corticosterone after being placed in a foster nest, also increased their begging. This is the first direct experimental test suggesting that hormonal control of chick begging as an index of condition, forms a mechanism controlling parental provisioning in tubenosed seabirds. We suggest that chick behaviour can explain a substantial part of the variation in growth patterns observed between individual birds.

Hormonal regulation of begging

The effect of hormones on begging behaviour of chicks has so far been studied in very few avian species (summarized in Schwabl & Lipar 2002). Two types of steroid hormones (corticosterone produced by chicks and maternal testosterone) have been found to influence begging behaviour. Because begging is the first co-ordinated behaviour of altricial chicks after hatching, maternal hormones 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 after hatching. There is, however, considerable potential for altricial nestlings to produce their own testosterone (Adkins-Regan *et al.* 1990), and this may be particularly relevant for chicks with a long nestling period, such as tubenosed seabirds.

The base levels and dynamics of steroid hormones of seabird chicks are so far not 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 in Quillfeldt *et al.* 2004, Red-legged kittiwake *Rissa brevirostris* in Kitaysky *et al.* 2001b; Black-legged kittiwake in Kitaysky *et al.* 1999; Blue-footed booby *Sula nebouxii* in Nuñez de la Mora *et al.* 1996). An increase of baseline corticosterone levels in response to food deprivation of days to weeks has been demonstrated experimentally in the latter three species. In contrast, 3 to 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, only increasing corticosterone towards the end of the fast of 4 to 6 months (Le Ninan *et al.* 1988). Testosterone was undetectable (below 0.06ng/ml) in 15-20-d-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).

There are only two previous studies including the analysis of hormones and begging in seabirds, to our knowledge, one focussing on testosterone (Eising & Groothuis 2003) and one on corticosterone (Kitaysky *et al.* 1999, 2001a,b, 2003). Maternal androgens were studied in Black-headed gulls, *Larus ridibundus* (Eising & Groothuis 2003), where chicks hatched from testosterone-injected eggs begged more frequently. In Black-legged kittiwakes *Rissa tridactyla*, experimentally food-deprived chicks had elevated corticosterone levels (Kitaysky *et al.* 1999, 2001b) and corticosterone-implanted chicks begged more frequently than sham-implanted controls (Kitaysky *et al.* 2001a, Kitaysky *et al.* 2003), thus suggesting that corticosterone might provide a mechanistic link between the physiological condition and behavioural interactions among parents and their chicks. However, elevated corticosterone in Black-legged kittiwake chicks was not only associated with increased food intake, but had associated costs such as low growth efficiency and compromised cognitive abilities later in life (Kitaysky *et al.* 2003), suggesting that the juvenile physiological traits may be related to fitness of birds in subsequent life-history stages.

In the present study, chicks in a cross-fostering experiment 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 effects observed in the cross-fostering experiment in

terms of hormonal regulation were a decrease in corticosterone in initially light chicks, and a strong increase in testosterone in initially heavy chicks, faced with lower delivery rates. Only initially heavy chicks, which had a 50% increase in testosterone, altered their begging call intensity consistently. They increased their begging efforts twofold after being placed in foster nests with initially poor provisioning rates, while only slightly increasing their corticosterone levels, which were not statistically different from controls. Therefore, endogenously produced testosterone seemed to have a stronger effect on begging than corticosterone.

This is further supported by evidence from the initially light chicks. In the control period, light chicks did not have higher rates of begging or higher begging call numbers than controls despite 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.

We were also interested in diurnal patterns of hormones in chicks of Thin-billed prions, which are fed during the night. Corticosterone was elevated at midnight (12.1 ng/ml) compared to daytime levels (3.33 ng/ml), while testosterone remained unchanged. The pattern of corticosterone is in contrast to the diel rhythms of plasma corticosterone in diurnal bird species where basal plasma corticosterone levels peak in the early morning, before the active period begins (Breuner et al. 1999; Romero & Remage-Healey 2000, Tarlow et al. 2003). This pattern has been described as 'pre-active peak' (Breuner et al. 1999; Romero & Remage-Healey 2000). Corticosterone is intimately 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 difference found in the present study may be related to the feeding regime, with chicks being fed at night.

Regulation of provisioning

Chicks of pelagic seabirds may accumulate large lipid reserves, attaining peak masses of nearly twice their parents mass partway through the growth period. This nestling obesity has stimulated much discussion, because it seems that parents are provisioning at rates much higher than necessary for successful fledging. At the end of nestling development, chicks lose mass and fledge close to 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 seabird chicks.

The initial body condition difference of 24% was reduced to 10% during the experimental period of ten days. Interestingly, both experimental groups were fed more than control chicks (Fig. 1), 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 were due to the higher delivery rates of the foster parents compared to the natural parents.

In contrast, heavy chicks increased their begging rates twofold and although they lost 8% of their initial body condition, they had the highest feeding rates of all groups. This is remarkable, because it means that parents with the poorest initial provisioning rates were stimulated by chick begging to deliver the highest feeding rates of all groups during the experimental period. The data also indicate that heavy chicks could afford the cost (assuming begging is costly) of increased begging, but light ones couldn't. Clearly, the increase in delivery rates was controlled by the behaviour of the chicks in this case. This result is in line with brood manipulation experiments of passerines which have demonstrated that parents increase their provisioning rates in response to increased brood sizes (e.g. Wright & Cuthill 1990). This suggests 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 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). However, the parental condition is also variable and chicks must be sensitive to such variation, and must adjust their behaviour appropriately, as 'low investment coming from a parent in poor condition has a different meaning than low investment coming from a parent in good condition' (Trivers 1974). In the cross-fostering experiment in the present study, evidence of behavioural adjustment, as predicted by parent-offspring conflict, was seen. In particular, poorly provisioning parents did not invest at the maximum possible rate, and increased provisioning as the apparent need of the chicks increased. Nor did heavy chicks beg at maximum rate in their original nests, but they only increased begging in the foster nests. Chicks and adults of tubenosed seabirds can identify their own nests by smell (Mínguez 1997, Bonadonna *et al.* 2004), and adults use this to return to their burrows and to find their chicks. 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 during the pre-fledging period simply by strong nest-site attachment (Redondo 1993). In the cross-fostering experiment, 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 with unfamiliar smell. It is therefore possible that the increase in begging in the chicks of the heavy group was possible because they were exploiting unrelated parents, and did not need to be sensitive to the adults body condition.

The study of begging in other tubenosed seabirds (Quillfeldt 2002, Quillfeldt *et al.* *In Press*, Quillfeldt & Masello *unpubl. data*) also highlighted individual differences in chick calling behaviour. After controlling for the effect of body condition, 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, in order to allow offspring and parental strategies to co-evolve and the conflict to be evolutionarily resolved, and there is evidence from a variety of animals that such variation exists (Kölliker & Richner 2001, Agrawal *et al.* 2001). Further studies are now needed on the origins of the hormonal and behavioural differences between individuals, its possible heritability, the influence of environmental variability and the costs incurred through such mechanisms which might explain hormone control of begging and signal honesty.

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Table 1. Variation in first sessions of begging calls in Thin-billed prions. The mean rate of begging calls was measured over the whole session, while the maximum call rate was the highest rate that chicks sustained over a whole minute within a session. The first recorded session for each chick was used to test if begging call parameters were correlated. We found significant correlations between all combinations of call parameters except session duration and maximum begging rate (total call number vs. duration: $r=0.904$, $N=20$, $P<0.001$; total call number vs. maximum call rate: $r=0.502$, $N=24$, $P=0.012$; total call number vs. mean rate of calls: $r=0.824$, $N=24$, $P<0.001$; duration vs. maximum call rate: $r=0.306$, $N=24$, $P=0.146$; duration vs. mean rate of calls: $r=0.561$, $N=24$, $P=0.004$; maximum call rate vs. mean rate of calls: $r=0.730$, $N=24$, $P<0.001$).

Parameter	Mean \pm s.e.	Min	Max
Session duration (min)	12.2 \pm 0.5	1	27
Total call number	24.7 \pm 0.7	65	756
Mean call rate (calls/min)	307.7 \pm 17.6	9.3	37.6
Maximum call rate(calls/min)	37.2 \pm 1.0	13	63

Table 2. Differences between nests and the effect of current body condition on parameters of begging in Thin-billed prions: (a) the begging call rate (calls/min), (b) the total call number in begging sessions, (c) the maximum number of calls in one minute and (d) the duration of begging call sessions (GLIM).

Source	Type III Sum of Squares	df	Mean Square	F	t	P	η^2
(a) begging call rate (calls/min) of begging call sessions							
Nest	972.5	19	51.2	1.82		0.058	0.476
Body condition	203.6	1	203.6	7.23	-2.69	0.011	0.160
Error	1071.0	38	28.2				
Total	2265.9	58					
(b) total call number in begging call sessions							
Nest	623853.9	19	32834.4	3.07		0.002	0.605
Body condition	84074.9	1	84074.9	7.85	-2.8	0.008	0.171
Error	406754.7	38	10704.1				
Total	1126146.7	58					
(c) maximum number of calls in one minute							
Nest	2269.8	19	119.5	2.71		0.004	0.575
Body condition	409.8	1	409.8	9.30	-3.05	0.004	0.197
Error	1674.3	38	44.1				
Total	4271.7	58					
(d) duration of begging call sessions							
Nest	884.4	19	46.5	2.16		0.020	0.522
Body condition	62.0	1	62.0	2.91	-1.71	0.096	0.071
Error	809.4	38	21.3				
Total	1726.7	58					

Table 3. Effect of call parameters on the meal size in the night of recording in Thin-billed prions (GLIM, with "meal size" as dependent variable).

Source	Type III Sum of Squares	<i>df</i>	Mean Square	<i>F</i>	<i>t</i>	<i>P</i>	η^2
(a) begging call rate (calls/min) of begging call sessions							
Nest	815669.3	19	42930.0	1.26		0.268	0.386
Call rate	392826.3	1	392826.3	11.49	3.39	0.002	0.232
Error	1299106.2	38	34187.0				
Total	2148332.6	58					
(b) total call number in begging call sessions							
Nest	649264.8	19	34171.8	0.872		0.616	0.304
Call number	202643.9	1	202643.9	5.171	2.27	0.029	0.120
Error	1489288.6	38	39191.8				
Total	2148332.6	58					
(c) maximum number of calls in one minute							
Nest	600749.8	19	31618.4	0.780		0.72	0.281
Call number	151021.8	1	151021.8	3.724	1.93	0.061	0.089
Error	1540910.7	38	40550.3				
Total	2148332.6	58					
(d) duration (min) of begging call sessions							
Nest	452443.5	19	23812.8	0.535		0.927	0.211
Duration	136.5	1	136.5	0.003	0.06	0.956	0.000
Error	1691796.0	38	44520.9				
Total	2148332.6	58					

Table 4. Body condition, steroid hormone secretion and parameters of begging (mean \pm SE) of nestling Thin-billed prions in response to a cross-fostering experiment. The chicks of the heavy group were fostered in nests of initially light chicks and vice versa.

Parameter	Control chicks (n=10)	Heavy chicks (n=5 ^a)	t-test Control vs. Heavy	Light chicks (n=5)	t-test Control vs. Light
(a) Body condition					
Control period	99.4 \pm 2.2	112.1 \pm 2.1	t = -4.3, d.f.13, P = 0.001	88.8 \pm 2.5	t = 3.2, d.f.13, P = 0.009
Experimental period	99.9 \pm 3.1	104.5 \pm 4.2	t = -0.9, d.f.13, P = 0.401	94.7 \pm 4.1	t = 1.0, d.f.13, P = 0.345
Difference	0.5 \pm 2.5	-7.6 \pm 4.8	t = 1.8, d.f.13, P = 0.098	5.9 \pm 2.7	t = -1.3, d.f.13, P = 0.220
(b) Mean corticosterone (ng/ml)					
Control period	3.8 \pm 0.5	2.1 \pm 0.3	t = 3.0, d.f.12, P = 0.011	5.6 \pm 0.3	t = -3.0, d.f.13, P = 0.011
Experimental period	2.3 \pm 0.5	3.0 \pm 1.2	t = -0.6, d.f.13, P = 0.600	1.8 \pm 0.4	t = 0.8, d.f.13, P = 0.462
Difference	-1.7 \pm 0.7	1.3 \pm 1.4	t = -2.2, d.f.12, P = 0.054	-3.8 \pm 0.6	t = 2.3, d.f.13, P = 0.046
(c) Mean testosterone (ng/ml)					
Control period	0.114 \pm 0.012	0.112 \pm 0.020	t = 0.1, d.f.12, P = 0.932	0.080 \pm 0.012	t = 2.0, d.f.13, P = 0.066
Experimental period	0.137 \pm 0.012	0.176 \pm 0.011	t = -2.5, d.f.13, P = 0.030	0.120 \pm 0.020	t = 0.7, d.f.13, P = 0.499
Difference	0.016 \pm 0.011	0.067 \pm 0.017	t = -2.5, d.f.12, P = 0.030	0.040 \pm 0.012	t = -1.0, d.f.13, P = 0.333
(d) Begging call rate (calls/min)					
Control period	26.7 \pm 1.2	22.8 \pm 1.2	t = 2.3, d.f.13, P = 0.037	26.5 \pm 2.7	t = 0.1, d.f.13, P = 0.965
Experimental period	25.3 \pm 1.7	28.1 \pm 2.4	t = -0.9, d.f.13, P = 0.375	24.9 \pm 3.8	t = 0.1, d.f.13, P = 0.936
Difference	-2.4 \pm 1.4	5.3 \pm 3.4	t = -2.4, d.f.13, P = 0.030	-1.6 \pm 3.8	t = 0.2, d.f.13, P = 0.881
(e) Total number of begging calls					
Control period	327.1 \pm 28.0	276.5 \pm 40.0	t = 1.0, d.f.13, P = 0.333	367.9 \pm 53.6	t = -0.7, d.f.13, P = 0.525
Experimental period	336.5 \pm 33.3	537.4 \pm 111.3	t = -2.2, d.f.13, P = 0.043	357.9 \pm 86.4	t = -0.2, d.f.13, P = 0.826
Difference	9.4 \pm 31.1	260.9 \pm 126.3	t = -2.6, d.f.13, P = 0.023	-10.0 \pm 99.7	t = 0.2, d.f.13, P = 0.851

^aOne chick of the heavy experimental group was not blood sampled before cross-fostering, and the sample size for hormone samples is n=4.

Fig. 1. Feeding rates for control and experimental chicks in a cross-fostering experiment of Thin-billed prions. In the control period all chicks were fed in their own nests, while in the experimental period, five pairs of initially heavy and light chicks were exchanged between their nests. Control chicks remained in their original nests.

Fig. 2. Relationship between the change in body condition between the control period and the experimental period and the change in corticosterone of experimental chicks measured during the control and experimental periods during the cross-fostering experiment.

Fig. 3. Relationship between the change in hormone secretion between the control period and the experimental period and the change in the total number of begging calls during feeding sessions of experimental chicks during the cross-fostering experiment.

Fig. 1.

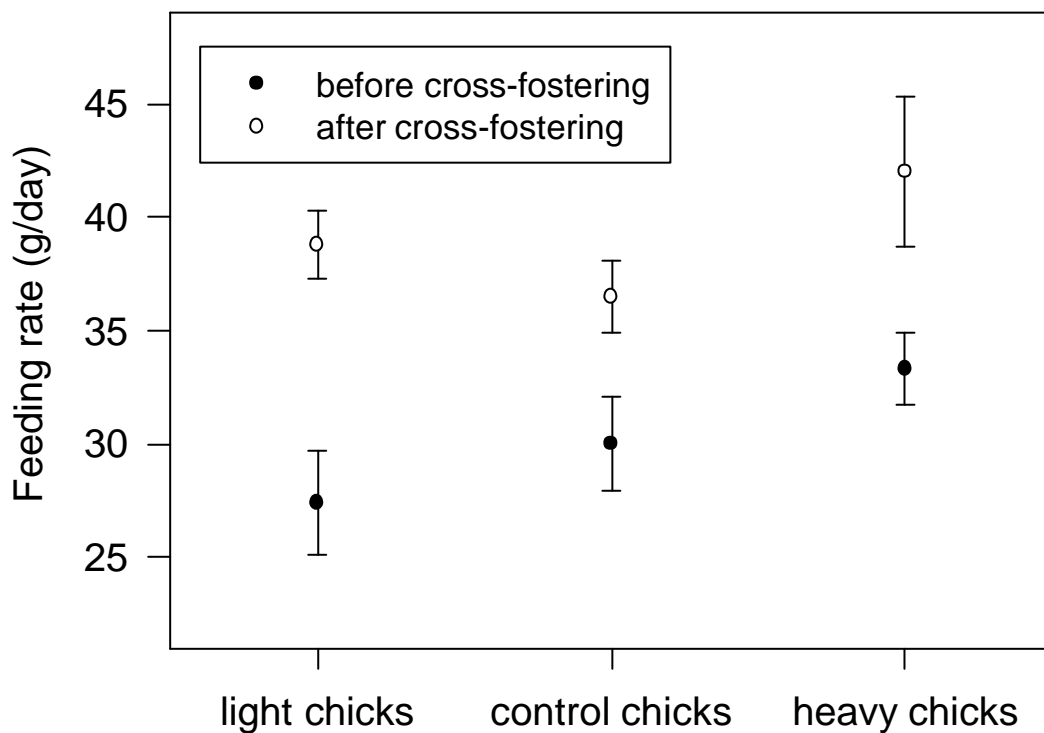


Fig. 2

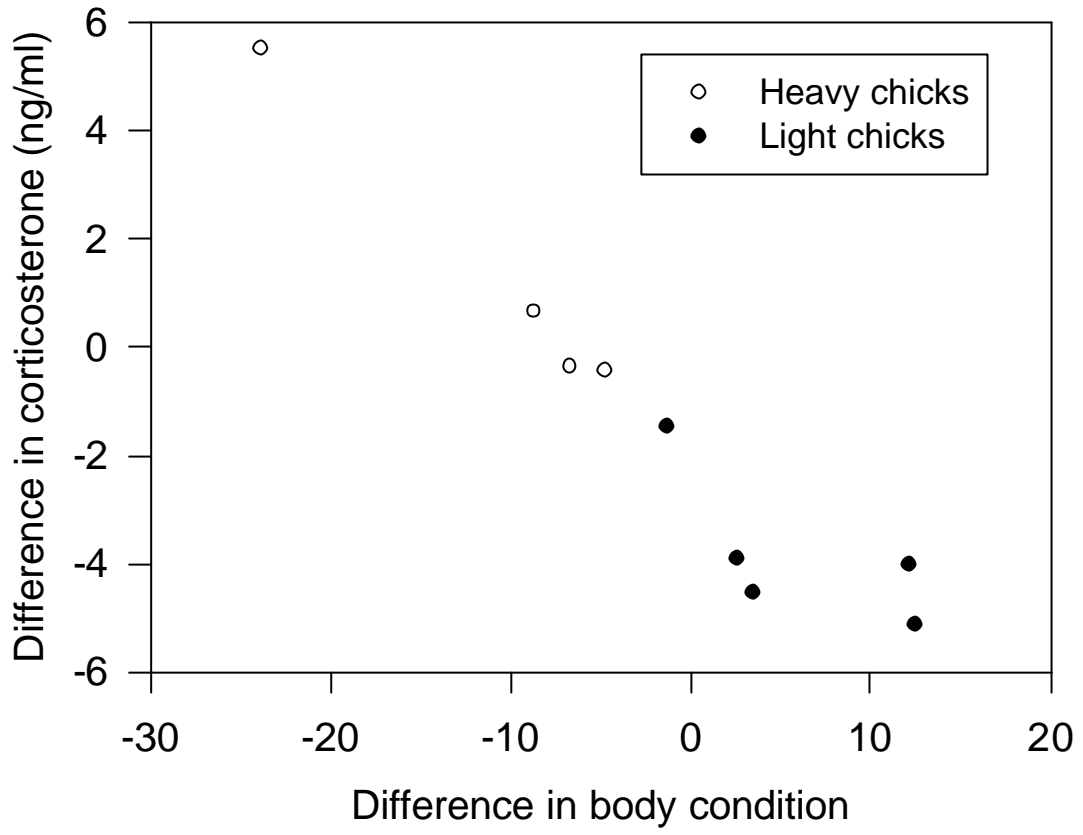


Fig. 3.

