Parental physiological condition and reproductive success in chinstrap penguins (*Pygoscelis antarctica*)

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Abstract   Recent studies suggest that parental resource allocation may be the most important factor explaining differences in reproductive output among parents. That said at least two different hypotheses of balance between parental foraging effort and resource allocation have been proposed. First, parents with high foraging effort have high reproductive success. Second, parents with higher allocation of resources to offspring have high reproductive success. We tested the second hypothesis using chinstrap penguins (*Pygoscelis antarctica*) as a model. We evaluated nutritional condition of the parents using blood urea, uric acid, creatine kinase, and cholesterol levels. We evaluated reproductive success according to total mass of the brood and asymmetries inside the brood. We measured the degree of asymmetry using weight and culmen length. Generalized linear models were used to examine relationships between adult plasma urea levels with year, nest position, and degree of asymmetry in chicks. Our results demonstrate that lighter broods were more asymmetric and associated with lower values of adult plasma urea, uric acid, and creatine kinase. We interpret these findings as evidence that the birds allocate fewer resources to their chicks than adults with more symmetric broods are.

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Introduction

The cost of reproduction is of fundamental importance in life-history evolution (Harshman and Zera 2007). A core idea is that the differential allocation of limited internal resources (the traditional 'Y' model of resource allocation where food input is shown at the base of the 'Y', and energy resources are allocated to reproduction versus the rest of the body) has a central role in the cost of reproduction and other life-history tradeoffs (Harshman and Zera 2007).

A major trade-off faced by breeding birds is resource allocation to offspring versus to self-maintenance, because strong parental investment may reduce survival of breeding adults, and thus overall lifetime reproductive success in long-lived organisms (Stearns 1976; Noordwijk and de Jong 1986). Regulation of reproductive effort in terms of provisioning offspring is particularly important for long-lived seabirds for which at sea foraging and meal delivery are energetically expensive and risky behavior (Chappell et al. 1993; Ydenberg 1994).

Food provisioning can limit growth and chick survival in penguins (Taylor and Roberts 1962; Ainley and Schlatter 1972; Boersma 1976, 1991; Cooper 1977; Williams 1980), but an excessive reproductive effort at one breeding attempt may decrease parental lifetime reproductive success or survival (Croxall and Rothery 1991; Wooller et al. 1992; Moreno 2003). Food provisioning involves two processes: resource acquisition through foraging activity, and resource allocation between self-maintenance and offspring's demands (Boggs 1992; Viñuela et al. 1996; Weimerskirch 1999). Balance between both

processes eventually determines the reproductive success of individuals.

Most penguin species lay more than one egg, and thus, face a situation in which they must distribute limited resources between several chicks. When resources are not sufficient to raise all hatched nestlings, brood reduction or a trade-off between number and quality of offspring may appear (Lack 1968; Moreno et al. 1998). Several mechanisms favoring differential allocation of resources to nestlings or facilitating brood reduction when available resources are not enough to raise all hatched chicks have been proposed, such as hatching asynchrony, sibling aggression, intra-clutch egg-size variation, or asymmetrical food distribution (Lack 1968; Moreno et al. 1994; Viñuela 1997, 1999; De León et al. 2001). It is known that chinstrap penguins raising two chicks have higher productivity than experimentally reduced single broods, but only at the cost of reduced growth rate and fledgling size of both nestlings (Moreno et al. 1998) and, as a consequence, at the cost of a decrease in the survival prospects (Moreno et al. 1999).

At least two different hypotheses about the balance between resource allocation and foraging effort have been proposed. Firstly, parents with high foraging effort are expected to exhibit high reproductive success (Pugesek 1995). Secondly, parents with higher allocation of resources to offspring should have high reproductive success (Hillström 1995; Wendeln and Becker 1999).

Recent studies have highlighted no correlation between the intensity of parental foraging effort and the offspring growth rates in the closely related Adélie penguin (*Pygoscelis adeliae*, Takahashi et al. 2003), suggesting that parental resource allocation rather than the foraging effort would be the most important factor explaining differences in the offspring performance. Additionally, Ballard et al. (2010) determined that parents in poor condition were not able to maintain or regain their own condition at the same time that they provisioned their young.

Here, we evaluate the relationship between parental nutritional condition and resource allocation among siblings in chinstrap penguins (*Pygoscelis antarctica*) with the principal aim of improving our understanding of the trade-off between reproductive investment and self-maintenance.

We estimated nutritional condition of the parents using plasma urea and uric acid levels. As is well known for many bird species (raptors, penguins, and gulls among others), when tissue protein sources are mobilized actively by starvation or undernourishment, urea and uric acid values increase (García-Rodríguez et al. 1987; Ferrer 1993; Alonso-Alvarez et al. 2002, 2003). The latter is caused by an increase in the nitrogenous excretion components released into the blood. Since both parameters are not sensitive to recent ingest (in contrast to glucose concentration for example), and increase and decrease in blood concentration is slow (García-Rodríguez et al. 1987; Ferrer 1990), they are good indicators not only of acute fasting, but also of mid-term nutritional condition (around 2 weeks according to García-Rodríguez et al. 1987; Alonso-Alvarez et al. 2003). For these reasons, these parameters have been used as indicators of nutritional condition in several species in different ecological contexts (Ferrer et al. 1987; Ferrer 1992, 1994; Alonso-Alvarez and Ferrer 2001; Casado et al. 2002; Balbontin and Ferrer 2005). Although large penguins show a fasting response that is clearly different from other birds (Cherel et al. 1988a, b, c), medium-small penguins, including chinstrap penguins, respond differently, showing a more rapid increase in urea level after fasting (Cherel et al. 1993).

Consequently, our hypothesis is that adults in poor nutritional state should have higher urea and uric acid levels and higher quality broods if parental resource allocation is an important factor driving reproductive output. However, if resource allocation is not an important factor, we expect that parents in poor nutritional conditions have lower quality broods, being reproductive output merely a reflection of the parent ability to obtain food provisioning. Additionally, we considered potential effect of the nest location in the colony, as penguins breeding in the center of the colony are presumably individuals of higher quality (Barbosa et al. 1997; Moreno et al. 1997; Minguez et al. 2001).

Materials and methods

Study area and species

The study was conducted at the Vapour Col chinstrap penguin rookery (approx. 20,000 breeding pairs) on Deception Island, South Shetlands, Antarctica (63°00′S, 60°40′W), during the austral summers of 1990–1991 and 1993–1994 (hereafter 1991 and 1994, respectively). Chinstrap penguin is a medium-size penguin (around 4 kg) with a maximum clutch size of two eggs (mean clutch size = 1.93).

During the two breeding seasons, we randomly selected and marked 293 nests (131 in 1991 and 162 in 1994) with numbered sticks at the end of the incubation period. Additionally, we tagged adults with metal flipper tags (standard 34 × 17 mm penguin bands, Lambournes Ltd., Solihull, UK). We sampled five sub-colonies with more than 150 breeding pairs each. We tried to visit nests daily before hatching, whenever harsh weather did not preclude fieldwork. As hatching is normally asynchronous in this species (modal asynchrony = 1 day, Moreno et al. 1994), we used the date of the first hatched nestling as the brood-hatching date. During periodic visits after hatching (daily whenever possible), we recorded nestling survival until they were 15 days old, when they reach thermoregulatory ability (Taylor 1985).

Parental nutritional condition

Alonso-Alvarez et al. (2003) stated that chinstrap penguins, as other penguins, showed different phases during starvation, including phase one during which a small decrease in mean urea values occurred. This reduction is due to the absence of external ingest of proteins and after four days in the chinstrap penguin (Alonso-Alvarez et al. 2003), start the second phase with a linear increases in urea level according to increasing catabolism. Nevertheless, in this penguin species, no statistical differences in urea or uric acid concentration were found between samples in control day and after 4 days of fasting, which is the beginning of the second phase (Alonso-Alvarez et al. 2003). Consequently, we can use all the values in the analyses.

All blood samples were obtained between 1100 and 1400 hour (solar time) to eliminate possible diurnal fluctuations caused by circadian rhythms (Ferrer 1990; Ferrer et al. 1994). We extracted up to 2 ml of blood from the brachial vein, into lithium heparin tubes. Centrifugation and plasma separation (10 min at 3,000 rpm) were done less than 6 h after the sample was drawn. Plasma analyses were carried out in a portable autoanalyser (Reflotron II, with the reagents recommended by Boehringer-Mannheim). Levels of uric acid and urea were determined. Additionally creatine kinase (CK) and cholesterol were also measured, the former related to muscular activity, stress and weight (Ferrer and Dobado-Berrios 1998; Casado et al. 2002) and the second with nutritional conditions in some bird species (Alonso-Alvarez and Ferrer 2001; Alonso-Alvarez et al. 2002, 2003). All analyses were carried out less than 8 h after the blood extraction. All blood measures were taken in milligrams per deciliter.

When the older chick was 15 days old, parents were still in the guard period of breeding (Moreno et al. 1994; Viñuela et al. 1996). In this period, one of the adults always protects the nestlings while the other is outside feeding at the sea. The adult coming from the sea replaces its mate on guarding duties, therefore male and female alternate periods of starvation on the nest with periods of foraging activity on the sea. Average duration of periods at the nest is 16.7 ± 0.9 h (Trivelpiece et al. 1987). In order to standardize the evaluation of the parental nutritional status, we took the blood sample from the absent adult when it returned from the sea. We also recorded sex and weight of the sampled adult. Sexes were determined according to morphometric measurements (Amat et al. 1993).

Sibling mass and asymmetry

Sibling size asymmetries are known to be related to different chick or juvenile survival (Boersma 1991; Seddon and Van Heezik 1991; Williams and Croxall 1991; Moreno et al.

1999). During the two breeding seasons, 28 nests (14 in 1991 and 14 in 1994) were randomly selected. The nests that we selected were in different sites of the colony, but all of them contained two eggs and later two nestlings. Nests were selected among those that hatched the same day to avoid confusing effect of hatching date on growth speed and general breeding phenology (Moreno et al. 1994; De León et al. 2001). Nests were assigned to one of two categories: "edge," where nests occupied locations in the external ring of nests in the colony; and "center," where nests were at least two nests away from the colony edge. Nestlings were weighed and measured (culmen to the nearest 0.1 mm with digital calipers) when the older one was 15 days old (around 1,150 g).

We used total weight of the brood (the sum of both chicks) as a proxy of total adult investment. We measured the degree of asymmetry using body mass and culmen length. Culmen length was selected as good estimator of growth in this species (Moreno et al. 1994; 1998). An index of intra-brood size asymmetry was obtained dividing the weight or the length of the culmen of the biggest chick by weight or culmen length of the smallest chick. In this species, there is no significant relationship between hatching asynchrony and the subsequent size asymmetry in nestlings (Moreno et al. 1994), with reversal in size hierarchy being relatively common (Moreno et al. 1994; Viñuela et al. 1996).

Statistical analyses

We used linear regression models to perform most of the parametric analyses. The data were analyzed to evaluate possible relationships between adult nutritional status and the degree of asymmetry in 15-day-old nestlings as dependent variable. Because one of the factors affecting CK plasma concentration is the weight, we conducted a multiple regression analysis including weight of the adult and CK level. In all the regression analyses, normal distribution of data and residuals were tested. We used ANOVA to evaluate potential differences in weight and plasma parameters between sexes in adults.

Generalized linear models (GLMs) were used to evaluate the effects of year, nest position, and chick asymmetry on parental plasma urea level using normal distribution and log-link function. All tests were 2-tailed. Statistica 7.0 software statistical package was used (Stat Soft Inc. 2004) to perform statistical analyses. We considered an alpha level of 0.05 to assess significance of the results.

Ethical standards

Procedures used in this study comply with the current laws for working in Antarctica. Permission to work in the study area and for penguin handling was granted by the Spanish Polar Committee.

Results

Overall, we measured 28 adults when returning from the sea for food provisioning, 13 males and 15 females (mean weight = 3,738 g $\pm$ 238). We detected no differences according to sex in weight (one way ANOVA $F_{1,26} = 0.16$, $P = 0.692$) nor in plasma urea concentrations (mean urea values: males = 13.01 mg/dl, females = 14.46 mg/dl ANOVA, $F_{1,26} = 0.348$, $P = 0.559$). Neither uric acid, (mean values: males = 9.36 mg/dl, females = 9.65 mg/dl ANOVA, $F_{1,26} = 0.054$, $P = 0.817$), CK (mean values: males = 363.84 mg/dl, females = 443.46 mg/dl ANOVA, $F_{1,26} = 1.947$, $P = 0.174$), or cholesterol (mean urea values: males = 225.15 mg/dl, females = 214.46 mg/dl ANOVA, $F_{1,26} = 0.307$, $P = 0.509$) showed differences between sexes.

The corresponding 28 broods were measured for asymmetry. Weight of nestlings varied between 820 and 1,400 g (mean = 1,128.7 $\pm$ 130.57) for the larger chicks and between 420 and 1,200 g for the smaller ones (mean = 803.75 $\pm$ 250.21). Total body mass of the brood was between 1,470 and 2,600 g (mean = 2,072.8 $\pm$ 352). The degree of weight asymmetry varied between 1.00 and 2.52 (mean = 1.51 $\pm$ 0.523). The degree of culmen asymmetry varied between 1.00 and 1.24 (mean = 1.12 $\pm$ 0.080).

Total mass of the brood was negatively related with weight asymmetry between siblings ($r = -0.51, n = 28, P = 0.005$), showing that broods with higher total weights were those with less asymmetric siblings. Brood total weight was related with weight of the smallest sibling ($r = 0.40, n = 28, P = 0.035$), but not with the biggest one ($r = -0.20, n = 28, P = 0.286$). Consequently, asymmetries appeared to be produced mainly by a reduction in the size of the second chick. Sibling weight asymmetry was positively related with sibling culmen asymmetry ($r = 0.419, n = 28, P = 0.026$). Culmen asymmetry was significantly related with total mass of the brood ($r = -0.428, n = 28, P = 0.029$) with higher degree of asymmetry as lower the total weight of the brood was.

Adult urea plasma concentration was positively related with the total mass of the brood ($r = 0.62, n = 28, P < 0.001$, Fig. 1), with parents in better nutritional condition having lower values of total brood weight. A negative significant relationship between urea plasma concentration in adults and the degree of weight asymmetry in the chicks was found, with parents with more asymmetric chicks showing lower values of urea ($r = -0.50, n = 28, P = 0.006$). Similarly, parent urea level was negatively related to culmen asymmetry ($r = -0.697, n = 28, P < 0.001$, Fig. 2). In other words, parents with more asymmetric young were in better nutritional condition.

Adult uric acid plasma concentration also was positively related with the total mass of the brood ($r = 0.41, n = 28, P = 0.029$) and negatively related to culmen asymmetry ($r = -0.66, n = 28, P < 0.001$). No relationship was
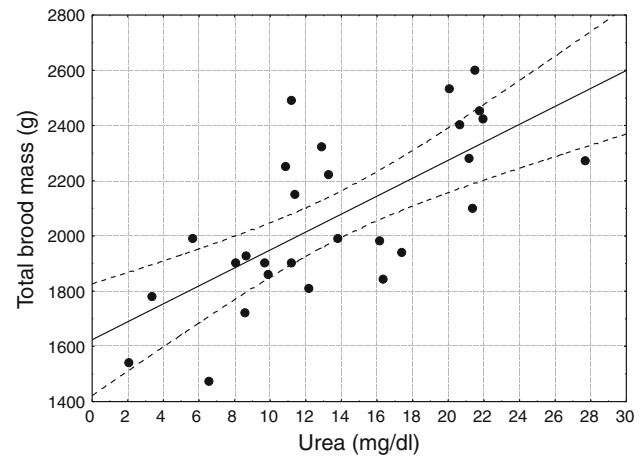

Fig. 1 Linear regression model between adult nutritional status (urea level) and total mass of the brood (weight, $r = 0.62$, $n = 28$, $P < 0.001$)
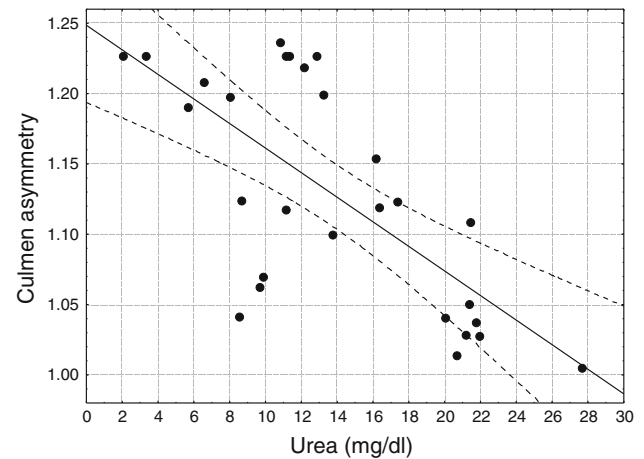

Fig. 2 Linear regression model between adult nutritional status (urea) and degree of asymmetry in chicks (dividing the length of the culmen of the biggest chick by culmen length of the smallest chick; culmen $r = -0.697$, $n = 28$, $P < 0.001$)

found between cholesterol and culmen asymmetry of the chicks ($r = 0.107$, $n = 28$, $P = 0.585$). As one of the factor affecting CK plasma concentration is the weight, we conducted a multiple regression including weight of the adult and CK level. Again, the degree of culmen asymmetry was negatively related to CK concentration ($r = -0.53$, $n = 28$, $P = 0.005$). The weight of the adults was not related to weight ($r = -0.12$, $n = 28$, $P = 0.540$) or culmen degrees of asymmetry of the chicks ($r = 0.022$, $n = 28$, $P = 0.450$).

The degree of culmen asymmetry was marginally related to nest position within the colony (GLM normal distribution and log-link function, Wald statistic 4.04, $P = 0.044$), with broods in the edge of the colony showing
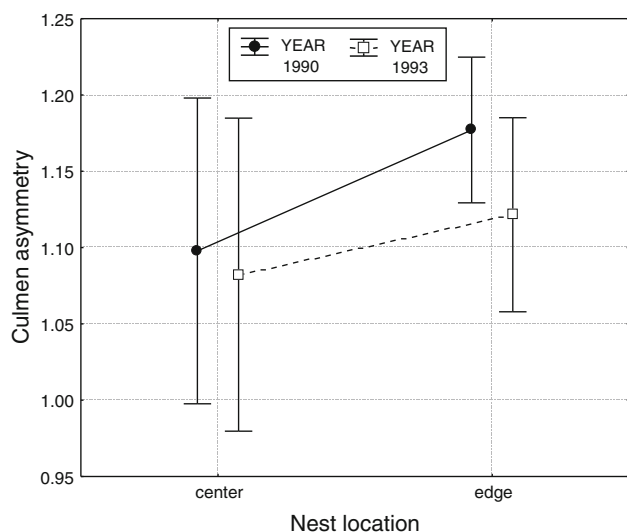
Fig. 3 Asymmetries in culmen length (length of the culmen of the biggest chick divided by culmen length of the smallest chick) between chicks according to nest location in 1991 and 1994

Table 1 GLM (normal distribution and log-link function) to evaluate the effect on parental plasma urea level on chick asymmetries, year and nest location

	df	Wald	*P*
Intercept	1	82.26	<0.001
Culmen asymmetry	1	22.14	<0.001
Weight asymmetry	1	4.01	0.045
Year	1	0.39	0.531
Nest location	1	0.39	0.530
Year*location	1	11.89	<0.001

Chick asymmetries were estimated dividing the weight or the length of the culmen of the biggest chick by weight or culmen length of the smallest chick

higher asymmetries than those in the center. Higher differences in culmen length between chicks according to nest location were found in 1991 than in 1994 (Fig. 3).

Adult urea levels were related to weight asymmetry, culmen asymmetry, and the interaction between year and location of the nest, being not affected by nest position or year (Table 1). Parents were in poor conditions in central nests during 1993, a good year according to productivity and weather conditions.

Discussion

Brood mass was related to parental physiological condition with parents rearing heavier chicks exhibiting reduced condition in comparison with parents of lighter broods. Asymmetry in weight is negatively related to the total weight of both young in the brood, suggesting that asymmetry is caused mostly by the smaller size and weight of the smallest chick, being size and weight of the biggest similar among broods. Consequently, asymmetries inside the brood seem to be related with total parental investment; those parents investing less obtained young that are more asymmetric. Total body mass of the broods and degree of asymmetry in both weight and culmen length were related with nutritional condition of the adults, with those adults raising heavier broods with more symmetric nestlings being in poorer nutritional conditions. These results support resource allocation hypothesis as parental raising heavier broods with more symmetric young seems to be in poorer nutritional conditions than those raising smaller and less symmetric ones. Overall, the results suggest that those adults raising more symmetric siblings could be allocating more resources on their brood at the cost of its own physical condition.

Sibling asymmetry may be related to sex of the chicks, because males are larger in this species, but no sexual differences in size are detected until nestlings are 25 days old (Fargallo et al. 2006). Thus, although we do not know the sex of chicks in this study, this factor should not be determining the degree of sibling asymmetries in the 15-day-old chicks. On the contrary, sibling asymmetries at these ages would primarily depend on food allocation patterns carried out by the parents.

Additionally, we found differences in the degree of sibling asymmetry according to nest location, with central nests producing more symmetric young. It is known that penguins breeding in the center of the colony are presumably individuals of higher quality, since they have larger bill size, lay eggs earlier, and have larger clutches than those nesting at the edge of the colony (Barbosa et al. 1997; Moreno et al. 1997; Minguez et al. 2001). Central nesters in our study colony also exhibited larger broods when the chicks were 15 days old (Ferrer et al. submitted). Therefore, our results suggest that potentially high-quality parents are achieving more symmetric chicks through a relatively greater allocation of resources on their offspring compare with resources assigned for their self-maintenance.

On the other hand, in the light of our results, the effect of nest location in the colony seems to be modulated by year. In fact, in 1991, differences in asymmetries between central and edge nests were 4 % higher than in 1994. According to published fecundity data for this colony (De León 2000), 1991 was the poorest year for the period 1991–1996, with a mean productivity of 1.50 chicks per active nest. Analyzing meteorological parameters for the same period (Ferrer et al. submitted), 1991 was the year with the low wind chill (high wind speed and lower temperature) of the studied period. It seems, consequently, that during cold years, degree of asymmetry increases, indicating that adults breeding at the periphery are less able to invest too much in their chicks,

keeping themselves in better nutritional conditions. This interpretation is supported by the findings of Ballard et al. (2010). Their results showed that penguins regulated their condition depending on environmental and physiological factors, with impacts on the amount of food delivered to young and pre-fledging mass. During good years it appears that, the adults take more risks increasing resource allocation in their young even while deteriorating their own energy levels. This interpretation is supported by Lescroël et al. (2010) conclusions that the difference between high-and low-quality individuals (Adélies at least) is accentuated during difficult environmental conditions.

Maintaining low energy reserves in breeding penguins would mean a low buffering capacity to sudden changes in the environment (Norberg 1981; Coulson et al. 1983; Nur 1984; Lima 1986; Bryant 1987) as well as reduced survival and/or fecundity in subsequent breeding attempts (Røskaft 1985; Tinbergen 1987; Gustafsson and Sutherland 1988). The question remains whether this deterioration in nutritional condition of the parents, because of greater allocation of resources in their young, would have consequences in future breeding attempts in this species or whether it is related to age or even is an individual characteristic stable among years (Noordwijk and de Jong 1986; Wendeln and Becker 1999). As we arrived to the colony at the end of the incubation period, we do not know if the initial situation of those parents who invest more was better at the beginning of the breeding cycle, facilitating that they allocated more resources in their young (Norberg 1981). Neither do we know what the effect of this greater allocation of resource would have in the survival and future fitness of their young (Noordwijk and de Jong 1986). Additional long-term work on the same individuals would be necessary to understand how this trade-off is resolved. Another additional interesting point for future studies would also be to assess the contribution and condition of both parents from the same nests—it is possible that one member of the pair can compensate for the other's shortcomings, or that high-quality parents tend to match with one another and vice versa.

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