



Breeding status affects the hormonal and metabolic response to acute stress in a long-lived seabird, the king penguin



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ABSTRACT

Stress responses are suggested to physiologically underlie parental decisions promoting the redirection of behaviour away from offspring care when survival is jeopardized (e.g., when facing a predator). Besides this classical view, the “brood-value hypothesis” suggests that parents’ stress responses may be adaptively attenuated to increase fitness, ensuring continued breeding when the relative value of the brood is high. Here, we test the brood-value hypothesis in breeding king penguins (*Aptenodytes patagonicus*), long-lived seabirds for which the energy commitment to reproduction is high. We subjected birds at different breeding stages (courtship, incubation and chick brooding) to an acute 30-min capture stress and measured their hormonal (corticosterone, CORT) and metabolic (non-esterified fatty acid, NEFA) responses to stress. We found that CORT responses were markedly attenuated in chick-brooding birds when compared to earlier stages of breeding (courtship and incubation). In addition, NEFA responses appeared to be rapidly attenuated in incubating and brooding birds, but a progressive increase in NEFA plasma levels in courting birds suggested energy mobilization to deal with the threat. Our results support the idea that stress responses may constitute an important life-history mechanism mediating parental reproductive decisions in relation to their expected fitness outcome.

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1. Introduction

Because parents are limited both in the time and energy to invest into offspring, decision rules about breeding and parental care should be selected considering a trade-off between the relative value of current reproduction vs. that of expected future breeding opportunities (Williams, 1966; Trivers, 1972; Maynard-Smith, 1977). According to the reproductive value hypothesis, parents may invest more into parental care as the clutch or offspring age, because of the higher probability of progeny surviving until sexual maturity (Andersson et al., 1980; Clutton-Brock, 1991). Consistently, several studies have shown that parental investment may change with offspring age, i.e. with the relative reproductive value of the young (Andersson et al., 1980; Redondo and Carranza, 1989; Cézilly et al., 1994; Albrecht and Klvana, 2004). For instance, birds are known to increase the amount of parental nest defence as offspring age, both throughout the incubation (Sjöberg, 1994;

Albrecht and Klvana, 2004; Osiejuk and Kuczynski, 2007) and chick-brooding (Redondo and Carranza, 1989) periods.

Mechanistically, stress responses have been suggested to physiologically underpin parental decisions by promoting the redirection of behaviour away from offspring care when survival is jeopardized. Stress responses allow animals to cope with unpredictable environmental challenges (i.e. labile perturbations, reviewed in Wingfield, 2003) by rapidly mounting a series of physiological and behavioural modifications. For instance, increases in glucocorticoid hormones (mainly corticosterone CORT, in birds) may promote the mobilization of energy substrates required to deal with impending threats (e.g. approaching predator, inclement weather). Breeding parents may then redirect their energy investment towards survival, thereby reducing or giving-up altogether on parental duties (Wingfield et al., 1998). The latter should especially apply to long-lived species for which lifetime reproductive success depends more on adult survival than seasonal fecundity, individuals behaving as ‘prudent parents’ (Drent and Daan, 1980; Stearns, 1992). However, when the value of the current breeding attempt is high relative to that of future reproductions, stress responses may be attenuated to ensure reproduction is not abandoned (Wingfield and Sapolsky, 2003).

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The ‘brood value hypothesis’ suggests that the magnitude of stress responses to acute challenges should match the level of parental commitment to the brood (Wingfield et al., 1995; Lendvai et al., 2007; Lendvai and Chastel, 2008; Goutte et al., 2011a). When brood value is high, parental stress responses should be attenuated to ensure continued breeding. Over the past couple of decades, this idea has been tested in numerous studies, yet conclusions remain equivocal. Whereas some studies have found corticosterone stress responses to be attenuated at advanced stages of breeding (Holberton and Wingfield, 2003; Adams et al., 2005; Williams et al., 2008; Krause et al., 2015), when brood value is high (Goutte et al., 2011a; Schmid et al., 2013), when breeding opportunities are limited (Wingfield et al., 1995; Romero et al., 1997; Heidinger et al., 2006), when parental care towards the offspring is increased (Meddle et al., 2003), or in the sex investing more into parental care (O’Reilly and Wingfield, 2001); this does not always appear to be the case (Chastel et al., 2005; Angelier et al., 2009, 2013; Riou et al., 2010). Other studies have found stress responses to be modulated according to life-history stage (e.g., in breeding vs. non-breeding individuals: Romero, 2002; Romero et al., 2006), or shown that circulating glucocorticoid levels may play a role in determining the onset of breeding (Goutte et al., 2010, 2011b).

A better understanding of the mechanisms mediating parental decisions related to breeding would benefit from the joint study of glucocorticoid stress responses and associated metabolic responses. Specifically, studying metabolic responses such as the release of free fatty acids (NEFA) in response to acute stressors during different breeding stages should inform us on the modulation of energy substrate mobilization aimed at promoting adult survival, especially in animals relying on fat energy reserves because fasting during reproduction. Thus, in this study, we considered the hormonal and metabolic (energetic) responses to acute stress in relation to breeding status in the king penguin (*Aptenodytes patagonicus*).

King penguins provide an interesting model for testing this question. In this species, the energy commitment to reproduction is particularly high (Cherel et al., 1994; Groscolas and Robin, 2001). The reproductive cycle from egg-laying to chick fledging lasts for over a year, during which breeding parents alternate between periods of long-term fasting on land and periods foraging at sea (Stonehouse, 1960). Parents are only able to raise a single chick within a season and clutch replacement almost never occurs (Weimerskirch et al., 1992). Parental effort increases throughout the breeding season (Weimerskirch et al., 1992), as likely reflected by an increase in both baseline glucocorticoid levels (Viblanc et al., 2014; Bonier et al., 2009) and territorial defence (Côté, 2000). Due to the length of the breeding season, successful birds are constrained to breed late in the subsequent season, with virtually no chance of success (Weimerskirch et al., 1992). Given the above, one might expect the value of reproduction to increase with the advancing breeding season as the clutch or offspring age (Montgomerie and Weatherhead, 1988; Côté, 2000), and parents to be more committed to reproduction during later stages of breeding. Consistent with this hypothesis, we recently found that the “fight-or-flight” response (as measured by heart rate increase) of breeding birds to acute stressors was attenuated with advancing breeding (Viblanc et al., 2015). However, whether those short-term adrenergic-based changes reflect an overall modulation of bird stress to advancing breeding, especially in terms of hormonal responses and energy substrate mobilization, is unknown.

We thus examined the modulation of total corticosterone (CORT) and circulating non-esterified free fatty acid (NEFA) responses to acute 30-min captures on breeding birds at the stages of courtship, incubation and chick brooding, of expected increasing reproductive value. In fasting penguins, NEFA plasma levels are a

good index of fat store mobilization (Groscolas, 1986; Cherel et al., 1988; Groscolas et al., 2008; Corbel et al., 2010). Baseline NEFA levels remain steady during phase II of fasting, increase at the transition from phase II to phase III, and decrease again when fat stores are close to exhaustion (Groscolas, 1986; Cherel et al., 1988). If stress responses are attenuated to prevent brood desertion when reproductive value is high, we expect CORT responses and energy substrate mobilization (as reflected in blood NEFA) to be highest during courtship, intermediate during incubation and lowest during chick brooding. The joint consideration of hormonal and metabolic responses to stress is expected to provide a relatively complete overview of the potential fine-tuning of stress responses to changes in breeding status.

2. Methods

2.1. Study animals

King penguins were studied on Possession Island, Crozet Archipelago (46°25’S, 51°45’E). During the 2010–2011 breeding season, we measured the adrenocortical and metabolic response of breeding birds to an acute and standardized capture-immobilization stress. Birds were sampled at three stages of the breeding cycle that differed in the amount of time and effort invested into the current breeding attempt: (1) at the very onset of reproduction during courtship when birds arrived ashore to breed, (2) during the first incubation shift (beginning or end), and (3) when birds were brooding a young non-thermally emancipated chick.

Twelve birds were stressed at each breeding stage, each bird being stressed only once. Courting birds were stressed while searching for a partner (songs, displays) on the beach adjacent to the breeding colony shortly after having arrived ashore for breeding. When capturing courting birds, we always caught the largest member of pair, and thus all courting birds were most likely males (as indeed confirmed by their morphometric measurements; average mass (mean \pm s.d.) = 13.4 \pm 0.8 kg; average wing length = 335.6 \pm 7.6 mm; average beak length = 135.9 \pm 4.5 mm; see Fahlman et al., 2006). In order to obtain birds at the onset and end of the first incubation shift, we marked 24 non-incubating pairs on the belly from a 1-m distance with spray animal dye (Procimark[®], Kruuse, Langeskov, Denmark), once settled on their breeding territory. We then performed daily visual observations at a distance using binoculars. The first time one member of the pair was observed alone incubating an egg, it was identified as a male at day 1 of incubation (Stonehouse, 1960; Weimerskirch et al., 1992; Descamps et al., 2002). Twelve males were stressed the next day (day 2 of incubation), while the other twelve were monitored until close to the end of the incubation shift, when they were stressed. Since the average duration of the first incubation shift is 16 days (Weimerskirch et al., 1992), we stressed those birds on day 15 of the shift to avoid their premature departure to sea. Brooding birds were stressed when caring for a small chick of approximately 10 days of age or less (as could be visually inferred from its size) and kept in their brood-pouch. This time period corresponds to the first brooding stage after hatching, during which the male is typically the one tending the chick (Stonehouse, 1960; Weimerskirch et al., 1992; Descamps et al., 2002). To avoid further displacing and disturbing incubating and brooding birds and risking breeding abandonment, we did not obtain any mass or size measurements for those groups.

The adrenocortical response was estimated from changes in the plasma concentration of total corticosterone and the metabolic response was determined from changes in the plasma concentration of non-esterified fatty acids, a good index of metabolic response to stress in penguins (Corbel et al., 2010) (see below).

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