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Protracted treatment with corticosterone reduces breeding success in a long-lived bird

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ABSTRACT

Determining the physiological mechanisms underpinning life-history decisions is essential for understanding the constraints under which life-history strategies can evolve. In long-lived species, where the residual reproductive value of breeders is high, adult survival is a key contributor to lifetime reproductive success. We therefore expect that when adult survival is compromised during reproduction, mechanisms will evolve to redirect resources away from reproduction, with implications for reproductive hormones, adult body mass, nest attendance behaviour and breeding success. We investigated whether manipulating corticosterone, to simulate exposure to an environmental stressor, affected the secretion of prolactin and breeding success in the black-legged kittiwake *Rissa tridactyla*. We used implanted Alzet® osmotic pumps to administer corticosterone to incubating kittiwakes at a constant rate over a period of approximately 8 days. Manipulated birds were compared with sham implanted birds and control birds, which had no implants. There was no significant difference in the body mass of captured individuals at the time of implantation and implant removal. Corticosterone-implanted males showed lower nest attendance during the chick rearing period compared to sham-implanted males; the opposite pattern was found in females. Corticosterone treated birds showed a marginally significant reduction in breeding success compared to sham-implanted individuals, with all failures occurring at least 1 week after implant removal. However, prolactin concentrations at implant removal were not significantly different from initial values. We were unable to measure the profile of change in corticosterone during the experiment. However, our results suggest a delayed effect of elevated corticosterone on breeding success rather than an immediate suppression of prolactin concentrations causing premature failure.

1. Introduction

Life-history theory predicts that, when resources are limiting, trade-offs occur between reproductive investment in the current breeding opportunity and self-maintenance to preserve future breeding opportunities (Stearns, 1977). In long-lived species, in which the success of any one breeding event is a relatively small component of lifetime reproductive success, allocation decisions that favour parent rather than offspring survival are expected (reviewed in Linden and Møller (1989)). The emergency life-history stage modulates the physiology and behaviour of organisms, through redirecting energy away from non-essential physiology and behaviours, such as reproduction or immune response, towards those needed for survival (reviewed in Wingfield et al. (1998)).

The emergency life-history stage involves the elevation of corticosterone—the main glucocorticoid in birds—in response to the activation of the hypothalamic–pituitary–adrenal axis (Wingfield et al., 1998). Chronic stress results from long-term exposure to a stressor, often resulting in negative fitness consequences such as low productivity, suppressed immunity and inhibited growth, rather than the short-term benefits of the emergency life-history stage, associated with acute stress. During chronic stress the duration of both the stressor and the consequences for an animal's physiology are long-lasting (Boonstra, 2013), resulting in sustained elevations of corticosterone. However, when corticosterone concentrations increase above baseline, the rate of passive clearance increases and active negative feedback reduces endogenous production (Sapolsky et al., 2000; Rich and Romero, 2005; Romero

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et al., 2005). This means that corticosterone is not maintained at stress-induced concentrations for long periods of time and therefore reduces the negative fitness consequences of long-lasting elevated corticosterone (Sapolsky et al., 2000; Romero, 2002).

Changes in corticosterone concentrations have a variety of implications for parental behaviour (reviewed in Crossin et al. (2012), Crespi et al. (2013)). Baseline concentrations of corticosterone can be positively correlated with parental behaviour ('corticosterone-adaptation hypothesis') through stimulatory effects on foraging behaviour, which enhance provisioning to chicks (Kitaysky et al., 2001; Angelier and Chastel, 2009). On the other hand, protracted stress-induced elevations of corticosterone suppress parental behaviour ('corticosterone-induced reproductive conflict'), causing the redirection of resources away from breeding and towards self-maintenance (Love et al., 2004).

Changes in corticosterone also have implications for the body mass of breeders. However, there is no clear prediction as to how chronic stress affects body mass. Correlational studies often show that increases in baseline corticosterone concentrations are associated with declines in body mass or body condition (i.e., size-corrected body mass e.g., Cherel et al., 1988, 1994; Kitaysky et al., 1999). However, Schultner et al. (2013a) showed that initial increases in baseline corticosterone concentrations were associated with an increase in fat reserves. Corticosterone secretion has also been found to be independent of changes in body condition in some species (e.g., Silverin and Wingfield, 1982; Wingfield et al., 1999; Lormée et al., 2003).

Evidence regarding the mechanistic process that modulates the stress response during breeding is currently inconclusive. One potential mediator of the stress response is via changes in prolactin concentrations (Chastel et al., 2005, reviewed in Angelier and Chastel (2009)). Prolactin has a wide variety of roles throughout the vertebrates (Norris, 1980). In birds it promotes incubation and parental care, and is secreted in response to long photoperiods and further by the presence of eggs and young in the nest (Dawson and Goldsmith, 1985; El Halawani et al., 1986). Chronic stress is expected to cause declines in reproductive hormones (Sapolsky, 2000) and, therefore, it is possible that corticosterone may disrupt prolactin secretion and reduce breeding behaviour such as nest attendance (Angelier et al., 2009a).

Studies to date that have looked for relationships between corticosterone and prolactin in long-lived seabirds have reached a range of often conflicting conclusions: some studies have found a negative correlation between the two hormones whilst others have found no relationship (reviewed in Angelier and Chastel (2009), Riou et al. (2010)). It has been suggested that, whilst the responses of corticosterone and prolactin to acute stress are not mechanistically linked, their responses to chronic stress are, with prolactin mediating the effect of corticosterone on breeding behaviour (reviewed in Angelier and Chastel (2009), Angelier et al. (2013)). Implantation of corticosterone in black-legged kittiwakes *Rissa tridactyla* breeding in Svalbard, Norway caused a reduction in prolactin concentrations, breeding success and nest attendance (Angelier et al., 2009a). In that study corticosterone was not successfully manipulated over a protracted period but rather increased to a peak on day one and had returned to baseline concentrations by day three (Angelier et al., 2009a). However, the responses of corticosterone and prolactin to chronic stress have not, to our knowledge, been tested.

The kittiwake is a long-lived seabird with a typical bi-parental care system, which has been studied in both the Atlantic and the Pacific with regards to its breeding biology and physiology (e.g., Golet et al., 2004; Angelier et al., 2009a; Goutte et al., 2010; Kitaysky et al., 2010). In this study, we used Alzet® osmotic pumps, which release substances at a constant rate over a number of days, in an attempt to elevate corticosterone concentrations over several days in a North Sea population of black-legged kittiwakes (hereafter 'kittiwake'). We hypothesised that this protracted elevation of corticosterone via Alzet® osmotic pumps would have a disruptive effect on breeding, specifically causing a short-term reduction in prolactin concentration and body mass, a reduction in nest attendance during the chick-rearing period, and lower breeding success by the end of the season.

2. Methods

2.1. Nest activity

270 kittiwake nests from 15 different plots on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11′ N, 02° 33′ W) were observed daily from laying to fledging in 2011 and for each nest we recorded the lay date, clutch size and either date of failure or number of chicks fledged (breeding success; Fig. 1).

2.2. Blood sampling of kittiwakes

38 kittiwakes (27 females and 11 males) were captured, each from different nests, during late incubation (May 25–May 30; 18 ± 5.4 (mean ± SD) days after laying; all birds were incubating at the time of initial capture; Fig. 1) using an eight metre long noose pole. A maximum of 1 ml of blood was taken from the wing vein using sterile 1 ml non-heparinised syringes. Samples were centrifuged, once the blood had been allowed to clot, and frozen as separate red blood cells and serum.

A dictaphone was used to precisely record the elapsed time between capture (i.e., when the noose was placed over a individual's head) and the end of blood sampling (individual sampling time), which we aimed to complete within 3 min of capture so that baseline, or near baseline, concentrations of corticosterone would be obtained (Romero and Reed, 2005). Individual sampling time was 2.7 ± 0.6 (mean ± SD) min, with 15% of samples being obtained within 2 min and 75% within 3 min. All samples were collected within 5.7 min. We also recorded the elapsed time between the extension of the noose pole towards the target individual and the lifting of the captured individual off its nest (capture time). Capture time was 1.2 ± 0.8 (mean ± SD) min with 56% of captures occurring within 1 min, 88% within 2 min and 98% within 3 min. In order to assess any impact of disturbance to individuals during the catching of other individuals at the same colony, individuals were ranked in the order that they were captured at a given site, on a given catching attempt. If a site was returned to later that day (>6 h later) or on the subsequent day, this was assumed to be a new catching attempt. There was a maximum of eight individuals captured per site on a given catching attempt.

2.3. Corticosterone manipulation in kittiwakes

For individuals already carrying a British Trust for Ornithology (BTO) metal ring the unique ring number was recorded and remaining individuals were ringed. Individuals were weighed to the nearest gram using a Pesola. Previous studies have used open-ended silastic tubes or self-degradable pellets to deliver corticosterone. These are unlikely to maintain protracted elevation such as that experienced during adverse environmental conditions (Romero et al., 2005; Newman et al., 2010; Thierry et al., 2013). Instead, we used Alzet® osmotic pumps (length: 3.0 cm; diameter: 0.7 cm; mass: 1.1 g; nominal volume: 200 μl; delivery period: 14 days; rate of delivery: 0.5 μl h^{-1}). These were inserted subcutaneously on the flank immediately anterior to the thigh, under local