General and Comparative Endocrinology 193 (2013) 112–120

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Corticosterone mediated costs of reproduction link current to future breeding

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ARTICLE INFO

Article history:
Received 6 December 2012
Revised 4 July 2013
Accepted 8 July 2013
Available online 26 July 2013

Keywords:
Breeding-moult overlap
Macronectes
Chick rearing
Feather corticosterone
Foraging behaviour

ABSTRACT

Life-history theory predicts that costs are associated with reproduction. One possible mediator of costs involves the secretion of glucocorticoid hormones, which in birds can be measured in feathers grown during the breeding period. Glucocorticoids mediate physiological responses to unpredictable environmental or other stressors, but they can also function as metabolic regulators during more predictable events such as reproduction. Here we show that corticosterone ("Cort") in feathers grown during the breeding season reflects reproductive effort in two Antarctic seabird species (giant petrels, *Macronectes* spp.). In females of both species, but not males, feather Cort ("fCort") was nearly 1.5-fold higher in successful than failed breeders (those that lost their eggs/chicks), suggesting a cost of successful reproduction, i.e., high fCort levels in females reflect the elevated plasma Cort levels required to support high metabolic demands of chick-rearing. Successful breeding also led to delayed moult prior to winter migration. The fCort levels and pre-migration moult score that we measured at the end of current breeding were predictive of subsequent reproductive effort in the following year. Birds with high fCort and a delayed initiation of moult were much more likely to defer breeding in the following year. Cort levels and the timing of moult thus provide a potential mechanism for the tradeoff between current and future reproduction.

1. Introduction

Life-history theory asserts that natural selection cannot simultaneously maximize both survival and reproductive activity, and assumes that reproduction has costs (Stearns, 1972). The physiological basis of these costs is not well understood, but glucocorticoid hormones (e.g., corticosterone) may be involved in mediating such costs. Well known for their role in allostasis and the physiological responses to unpredictable environmental stressors (Blas et al., 2007; MacDougall-Shackleton et al., 2009; Romero and Wikelski, 2001; Wingfield et al., 1998), glucocorticoids can trigger breeding desertion and failure if threshold levels are exceeded, as individuals must re-direct resources towards self-maintenance in order to cope with stressor at hand (Breuner et al., 2008). However, glucocorticoids also function as metabolic regulators during more predictable events, like migration and seasonal breeding, and can be positively correlated with measures of current reproductive effort (Crossin et al., 2012a; Hau and Beebe, 2011). Studies detailing the role of corticosterone in the regulation of parental care, via positive effects on foraging behaviour and provisioning effort, underscore its ubiquitous role in organismal fitness (Bonier et al., 2011; Crossin et al., 2012a; Love et al., 2004).

Not surprisingly, the relationships between glucocorticoids and fitness measures are complex and influenced by factors like age, breeding status, physiological condition, population, species, and ecology. Two recent reviews illustrate how variation in plasma levels of corticosterone (hereafter called "Cort"), at any single point in time, can be either positively, negatively, or non-significantly related to fitness or surrogates thereof (Bonier et al., 2009a; Breuner et al., 2008). Understanding the role of Cort in fitness, and predicting the direction of the relationship between the two, may depend on whether baseline or stress-induced plasma levels are examined. However, in studies where no relationship is observed (typically in studies examining seasonal phenomena), plasma Cort offers only a "snapshot" view of an individual's physiological condition (hours to day), which may be insufficient for resolving events operating over longer time-frames. A longer-term, integrated measure of Cort secretion and hypothalamo–pituitary–adrenal axis (HPA) activity has the potential to resolve Cort's role in broad temporal processes like seasonal migrations, reproduction, or transitions between these life-history stages, especially in situations where plasma Cort does not reveal any associations. Analysis of Cort in keratin-based

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http://dx.doi.org/10.1016/j.ygcen.2013.07.011

tissues (feathers, hair), which accumulate glucocorticoid hormones during growth (weeks to months), has been used recently to provide a more useful means for interpreting variation in broad-scale life-history events (birds Bortolotti et al., 2008, 2009; mammals (Fourie and Bernstein, 2011; Macbeth et al., 2010). The analysis of Cort in feathers (hereafter called ‘‘fCort’’) has the potential to increase our understanding of the mechanisms controlling avian life-histories (Bortolotti et al., 2008, 2009; Lattin et al., 2011).

Experimental studies of captive birds have confirmed that fCort levels can reflect high, or stress-induced, plasma Cort levels during the period when feathers are grown (Bortolotti et al., 2008; Lattin et al., 2011). Furthermore, variation in fCort has been linked to reproductive effort in captive partridges (*Alectoris rufa*) (Bortolotti et al., 2008). But only a small number of studies have linked natural variation in fCort to fitness measures (e.g., reproductive success) in free-living birds. Fairhurst et al. (2012) found that variation in parental investment by a seabird species (Cory's shearwaters, *Calonectris diomedea*) was reflected in fCort levels in the feathers of chicks. Specifically, they found that low foraging efficiency by parents led to a suppression or down-regulation of Cort secretion by chicks, which they interpreted as a buffer against nutritional stress and the deleterious effects of long-term HPA activation, resulting in lower fCort levels. Although fCort levels were not measured in the parent shearwaters, we might expect these to correlate positively with foraging effort (Angelier et al., 2008; Crossin et al., 2012a), and with chick growth (Bonier et al., 2011; Crossin et al., 2012a). More recently, Kouwenberg et al. (2013) show positive correlations between pre-breeding fCort levels and egg sizes in Atlantic puffins (*Fratercula arctica*), providing a link between winter foraging effort and reproductive effort.

Collectively, the studies by Bortolotti et al. (2008), Fairhurst et al. (2012), and Kouwenberg et al. (2013) provide growing evidence for a positive link between variation in fCort and fitness components in birds, but there is also an example of a negative fitness link. Koren et al. (2011) examined fCort levels in feathers grown during a post-breeding moult in sparrows (*Passer domesticus*) and found that elevated levels were related to lower overwinter survival. This study did not identify the underlying mechanism, but recent studies have shown that elevated Cort can both slow the rate of moult and negatively affect feather quality (DesRochers et al., 2009; Romero et al., 2005; Strochlic and Romero, 2008), including reductions in the insulating properties of feathers critical for survival at low winter temperatures.

Plasma Cort is usually down-regulated at the onset of post-breeding moult. As a catabolic steroid, this is presumably to avoid the breakdown of structural proteins at a time when anabolic processes are needed (e.g., new feather synthesis), as well as the Cort-dependent inhibition of new protein synthesis during feather growth (DesRochers et al., 2009). For species that moult during chick-rearing, how is the potential need to up-regulate baseline corticosterone in support of foraging and parental effort reconciled against the need to down-regulate it to avoid negative effects on feather growth? More importantly, what are the functional consequences of breeding activity and Cort secretion on the rate of new feather growth, fCort levels, future survival, and future breeding?

In this study, we test the hypothesis that fCort in breeding adults can provide an integrated measure of HPA activity in relation to current reproductive effort. We also hypothesize that fCort would be correlated with future reproductive effort. To address this, we took advantage of the unusual characteristic of giant petrels (*Macronectes* spp.), which unlike most birds (but see Bridge, 2006) begin moulting during incubation or early chick-rearing, and continue growing new feathers until the end of the breeding season (Crossin et al., 2012b; Hunter, 1984a), i.e., they exhibit a breeding-moult overlap, coincident with parental care. We measured both plasma Cort and fCort in feathers grown by parents during chick-rearing in year *x* (their current reproductive attempt), and compared levels in parent birds who lost their eggs or chicks earlier in the season. Comparisons between successful and failed breeders should reveal the HPA activity and Cort secretion needed to support investment in chick rearing. We therefore sampled successful and failed individuals from two species of giant petrels at the end of a breeding season (northern *Macronectes halli* and southern *Macronectes giganteus*). In addition to plasma and fort, we compared moult scores in successful and failed breeders. We then followed and recorded the survival and breeding activity of the same individuals over successive breeding seasons. By doing so, we could examine associations between fCort, plasma Cort, and feather moult during the current reproductive effort (year x), with future survival and reproductive decisions (breeding vs. deferral in year x + 1).

We predicted three things. (1) That reproductive success in year *x* would be positively related to fCort levels, based on an assumption that baseline Cort is up-regulated in successfully breeding birds, relative to failed breeders, to support the higher metabolic demands of parental care. Given its role in the stress response however, we expect the relationship between Cort and parental care measures to fit an inverse *U* function, wherein low levels of parental care can result from very low or very high levels (e.g., a stress response). But at the middle of this curve, high levels should be positively linked to parental care. (2) We also predicted that the relationship between Cort and reproductive effort would be more readily detected in feathers than in plasma, as feathers should integrate the hormonal signal over the extended period of feather growth coincident with incubation and chick-rearing. Finally (3) we predicted that a relationship between fCort levels and future breeding probability in year $x + 1$ would indicate a long-term cost of reproductive investment. Given that successfully breeding giant petrels in year *x* have a delayed or slower rate of moult and feather growth than failed breeders (Crossin et al., 2012b; Hunter, 1984a), we predicted that high fCort and delayed moult would provide a potential mechanism underlying the tradeoff between current and future reproduction.

2. Materials and methods

2.1. Study site and sample collection

Data were collected from northern and southern giant petrels breeding on Bird Island, South Georgia (54°00′S, 38°02′W) during chick-rearing in the the austral summer of 2008/09. Blood samples and moult scores were collected in 2008/09 only, but survival and subsequent breeding histories for all individuals were monitored closely during the 2009/10, 2010/11, and 2011/12 breeding seasons. Our principal aim was to link current breeding activity (2008/09 season) to future reproduction (2009/10 season). Given the high breeding site fidelity of giant petrels, we assumed that birds unobserved after the 2008/09 season had died at sea. Although we recognize that there could be alternative reasons for birds being unobserved, a precedent for this assumption was established by Foote et al.'s study of giant petrels (Foote et al., 2011).

Giant petrels lay only one egg, and parents share egg incubation and chick feeding duties nearly equally (Hunter, 1984b). Northern giant petrels laid from mid September to mid October, chicks hatched from mid November to mid December, and fledged from mid March to early April (Fig. 1). Southern giant petrels began laying in November, about 6 weeks later than northern giant petrels, and chicks hatched in January and fledged in late April to May. Birds with chicks were sampled on 5–13 March 2009, when chicks