Feather corticosterone as a measure of post-migratory stress physiology, and links to breeding fate.

Introduction

Life-history theory asserts that natural selection cannot simultaneously maximize both reproductive investment and survival, and so assumes that reproduction has costs (Stearns 1972). The physiological basis of these costs is not well understood, but glucocorticoid hormones (e.g. corticosterone, cortisol) may be involved in mediating these. Glucocorticoid “stress” hormones are well known for their role in allostasis and the physiological responses to unpredictable environmental events (Wingfield et al. 1998; Romero and Wikelski 2001; Blas et al. 2007; MacDougall-Shackleton et al. 2009), and 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 (Hau and Beebe 2011; Crossin et al. 2012). 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 (Love et al. 2004; Bonier et al. 2011; Crossin et al. 2012).

Traditionally, the analysis of corticosterone (hereafter “Cort”) in blood plasma has been the principal means for quantifying Cort levels. However, links between Cort and life-history or other fitness-related events can only generally be resolved within relatively short time-frames before metabolic clearance (days to weeks). The analysis of Cort in feathers (e.g. “fCort”) is emerging as a means for examining Cort secretion over longer time-frames, ranging from weeks to months (Bortolotti et al., 2008, 2009; Lattin et al., 2011). This opens the possibility for linking Cort secretion to life-history events operating over longer time-frames, like seasonal transitions (e.g. carryover effects). However, the fCort method is still in its infancy, and there is much debate, and indeed disagreement, about how to interpret results.

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Methods

Studies were conducted at Bird Island, South Georgia, where the British Antarctic Survey runs an on-going, long-term demographic monitoring program on the breeding activity and survival of individually ringed albatrosses and petrels. Within this program, I monitored individuals seabirds across years, and conducted studies that addressed the following two questions:

1. Does variation in fCort reflect current reproductive effort in a long-lived seabird?
2. Can fCort be used to link variation in winter migrations and spring breeding decisions?

Study 1

Giant petrels (*Macronectes spp.*) are unique in that they are among the minority of bird species that initiate moult whilst breeding, e.g. they exhibit an overlap between breeding and moult (Hunter 1985; Crossin et al. 2012b). We took advantage of this unique situation to explore the role of Cort across an entire breeding season in Northern (*M. halli*) and Southern (*M. giganteus*) giant petrels. Each season, parent giant petrels begin moult and the growth of new feathers about the time that their eggs begin to hatch. By collecting newly grown feathers from birds at the end of the breeding season, just prior to the fledging of chicks, fCort levels should reflect the amount of Cort secreted during the entire period coincident with chick-rearing. In other words, the fCort level should be integrated to reflect breeding effort. Furthermore, by comparing fCort levels in successful breeders versus failed breeders (those who lost their egg or chick), differences might be detectable.

This study’s principal aim is to determine whether variation in fCort can be used meaningfully to interpret variation in breeding success in giant petrels. This is an important first step because, as indicated earlier, there is still much controversy about fCort and its relevance to life-histories. To that end, we collected blood from all birds at the time of feather sampling, so that we could also assay plasma for Cort and compare plasma levels to feather levels.

This study is now complete and main results will be presented below.

Study 2

Having established a working relationship between fCort and breeding success, and a useful framework for interpreting variation in fCort levels, the next study will explore the links between migratory activity and subsequent breeding activity in black-browed and gray-headed albatrosses (*Thalassarche melanophrys* and *T. chrysostoma*, respectively). Specifically, this study will attempt to identify Cort (via fCort) as a key physiological mediator of migratory carryover effects onto spring breeding. The study of carryover effects (COEs) is presently a hot topic in ecology, and many studies have identified COEs on various aspects of reproduction, e.g. timing of breeding timing (Marra et al. 1998; Norris et al. 2004; Descamps et al. 2011; Harrison et al. 2011), breeding decision (Ebbinge and Spaans 1995; Crossin et al. 2012c), breeding output (Ebbinge and Spaans 1995; Sorenson et al. 2009), and breeding success (Baker et al. 2004; Inger et al. 2010; Crossin et al. 2012c). However, despite a long standing appreciation that physiological mechanisms must underlie COEs, we still know little about the endocrine and other factors responsible for generating these.

Black-browed and gray-headed albatrosses moult different feather groups at different times of the year. In winter, tail feathers (i.e. rectrices) are shed and grown anew. Thus, similar to the previous study of giant petrels, by collecting these newly grown rectrices upon arrival at their colonies at Bird Island, these should provide an integrated estimate of Cort that was secreted throughout the period of feather growth, coincident with the non-breeding migration in winter when birds are at sea. I will then examine whether fCort levels in these feather predict whether bird breed or not, which could be interpreted as a Cort-mediated carryover effect from migration to breeding.

All of the albatrosses in this study were also bearing geolocators, which were affixed to leg bands at the end of the previous breeding season. Collectively, this will allow me to link variation
in winter migration patterns and activity levels, to variation in fCort levels measured upon arrival at Bird Island, and breeding decision.

Ultimately I will analyzing and processing the geolocator data to generate migration histories for each individual bird, and assay the matched rectrices for fCort. This process is ongoing, and has suffered delays due to the biennial breeding pattern of the gray-headed albatrosses, which required several years to recover all individuals birds.

Results thus far, and Discussion

Study 1: The main result of this study is that fCort proved useful for explaining variation in breeding fate in the giant petrels. This result supports my principal aim, which was to show the utility of fCort in explaining life-history or fitness-related variation around events that operate over long (e.g. seasonal) time-frames. Figure 1 below shows two things of interest. First is that fCort showed clear differences between successful and failed breeders, but only in female birds. We suggest that the sexual segregation of foraging behaviour that occurs in giant petrels during the breeding season is one potential reason for this pattern (González-Solís et al. 2008; Phillips et al. 2011). Studies have shown that males tend to forage on local beaches for seal and penguin carrion, whilst females range pelagically to distant upwelling or frontal zones, which requires greater effort, especially when primary flight feathers are being moulted and re-grown at the same time. Given its role as a metabolic hormone with positive pleiotropic effects on locomotion and foraging behaviour, we interpret the higher fCort levels in successfully breeding females as an adaptation to foster foraging success and successful parental care.

The second point of interest is that plasma Cort did not show any association with breeding fate, in either sex or species. This provides additional support for the potential application and utility of fCort as a mediator of fitness-related events in studies where plasma might Cort fail to do so.

Given the importance of these results to the ongoing debate about fCort and its acceptance as a viable technique by ecologists and ecological physiologists/endocrinologists, my coauthors and I felt that it was essential to have this study reviewed by an endocrinological journal. It was thus submitted to, and recently accepted by, General and Comparative Endocrinology (Crossin et al. 2013).

Study 2, which is exploring the role of fCort as a key physiological mediator between migratory activity and breeding decisions in albatrosses, is being prepared for submission to Antarctic Science. This contribution will be one of the first to link positional telemetry, endocrine physiology, and breeding activity across life-history stages, thus providing a potential mechanism and driver of COEs in migratory seabirds.

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References


Fig 1. Corticosterone levels measured in feathers and blood plasma of Northern (*M. halli*) and Southern (*M. giganteus*) giant petrels breeding at Bird Island, South Georgia. Samples were collected late in the breeding season, prior to the fledging of chicks, and values are grouped according to species, sex, and breeding outcome (failed or successful). Columns represent least squares means which account for allometric covariation in body mass (ANCOVA). Error bars signify +SEM. Statistical significance was assessed at $\alpha=0.05$. This figure appears with additional results in Crossin et al. (2013).