



Seasonal patterns of prolactin and corticosterone secretion in an Antarctic seabird that moults during reproduction

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ABSTRACT

In avian species that have evolved life-history strategies wherein molt and breeding overlap, there are potential conflicts between the regulatory roles of baseline prolactin and corticosterone in parental care (positive) and moult (negative). We describe seasonal patterns of hormonal secretion, moult, and parental behaviour in sibling species of giant petrels (*Macronectes* spp.) which begin moult during the incubation/early chick-rearing stage of reproduction. With the exception of male Southern giant petrels (*Macronectes giganteus*), prolactin secretion and moult in Northern (*Macronectes halli*) and female Southern giant petrels conformed to those observed in all other avian species, with the initiation of moult coincident with decreases from peak prolactin levels. However, male Southern giant petrels began moulting early in incubation when prolactin was increasing and had not yet peaked, which suggests a requirement of prolactin for incubation behaviour and a dissociation of prolactin from moult. Corticosterone showed little seasonal variation and no relationship with moult. When comparing prolactin, corticosterone, and moult in failed vs. active breeders, we found that failed breeding enabled a more rapid down-regulation of prolactin, thus facilitating a more rapid moult. We present specific examples of the behavioural ecology of giant petrels which we conclude help mediate any potential hormonal conflicts between parental care and moult.

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1. Introduction

It has long been held that the avian annual cycle is structured so that reproduction and moult are temporally segregated, thereby minimising the potential for energetic or physiological conflict [9,25,33,34,40], and the idea that these two activities are mutually exclusive persists [7]. However, many avian species have evolved moulting strategies which overlap to varying degrees with reproduction, including seabirds [1,4,17,32,38,44], raptors [28,43], passerines [19,20,26,41] and shorebirds [27]. Here we use the extensive moult–breeding overlap that occurs in giant petrels (*Macronectes* spp. [30]) to further our understanding of the hormonal control of moult, and in particular to determine how birds resolve potential hormonal conflicts generated by ‘pleiotropic’ effects of prolactin and corticosterone in the regulation of parental care (positive regulatory effects) and moult (negative regulatory effects) [23,47].

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Experimental and descriptive studies with a variety of bird species (e.g. European starlings [*Sturnus vulgaris*], Mute swans [*Cygnus olos*]) have shown that the endocrine control of moult is regulated in part by the hormone prolactin [35], and specifically it is the decrease from seasonal peaks rather than some absolute threshold which signals the initiation of moult [9,15]. Immunization against vasoactive intestinal peptide, the prolactin-releasing hormone in birds, inhibits photoperiodically induced prolactin secretion and moult [12]; thus, moult generally cannot be readily disengaged from prolactin secretion [9]. However, prolactin also affects parental behaviour, particularly incubation behaviour in the form of egg defense and thermoregulation, and elevated plasma prolactin is maintained in many species until relatively late in chick-rearing to facilitate parental care [55]. Therefore, if high plasma prolactin levels actually inhibit the initiation of moult, this could explain why for many (but not all) birds moult tends to begin late in chick-rearing when parental care is waning [2,10,13,15]. In species exhibiting an overlap between parental care and moult, there is an apparent conflict due to the pleiotropic effects of prolactin. How can some species initiate moult without a decrease in prolactin (as suggested by [15])? Conversely, how can birds provide effective

parental care if prolactin decreases early in incubation/chick-rearing in order to initiate moult?

A similar conflict might emerge during a breeding–moult overlap via the pleiotropic effects of the glucocorticoid hormone corticosterone. In many respects, a physiological stress response should be ‘adaptive’ by increasing the likelihood that an individual will survive and cope with a transient environmental stressor, though over-stimulation due to chronic stress, or severe acute stressors, can lead to long-term negative effects [52]. Many studies of stress physiology have focused on the functional consequences of maximum or stress-induced corticosterone levels in response to acute stressors or unpredictable events [37,49,58–60]. The acute stress response mediates fairly rapid, short-term physiological and behavioural changes (e.g. the “emergency life history stage” [59]) to allow individuals to cope with environmental stressors, principally though a positive effect on locomotor and foraging behaviour with negative effects on reproduction. More recent attempts to place this work in the context of life-histories has highlighted the small number of studies that have linked variation in glucocorticoids to variation in fitness, fecundity, reproductive success or survival, either for baseline corticosterone [6] or stress-induced corticosterone levels [8]. Variation in corticosterone at any single point in time can be positively, negatively, or non-significantly related to surrogates of fitness [6,8] and the relationships can (not surprisingly) vary within individuals at different times in their life history.

Along these lines, recent studies have shown that baseline (i.e. not stress-induced) corticosterone secretion can be adaptively up-regulated during the reproductive season to facilitate high rates of provisioning for growing chicks [2,36]. However, corticosterone is usually down-regulated prior to the onset of the post-breeding moult, presumably to avoid the catabolism of structural proteins needed for feather synthesis, as well as the corticosterone-dependent inhibition of new protein synthesis during feather growth [16]. Indeed, baseline corticosterone tends to be low in migratory passerines undergoing prebasic moult, and the adrenocortical response to stress is also down-regulated [48,51]. How do birds exhibiting a breeding–moult overlap reconcile the need to up-regulate baseline corticosterone during chick-rearing to support foraging against the need to down-regulate it to avoid negative effects on moult (e.g. delayed moult, poor feather quality; [14,51])?

To address these questions, we present correlative data on the temporal patterns of prolactin and corticosterone secretion during the breeding–moult overlap in sibling species of giant petrels (*Macronectes* spp.) nesting sympatrically at a sub-Antarctic island. Giant petrels provide a good model for exploring the endocrine control of moult and the potential conflicts therein as both Northern (*Macronectes halli*) and Southern (*Macronectes giganteus*) giant petrels begin moulting their primary flight and body feathers towards the end of the incubation period or early-to-mid chick-rearing, though Southern males can begin moult during the initiation of incubation behaviours [30]. Hunter [30] speculated that the high availability of food resources and animal carrion might provide sufficient energy to facilitate both reproduction and moult, and due to sexual dimorphism in foraging behaviour this might favour males as they tend to forage more locally while females rely more on marine foraging [21]. Coupled with the fact that the two species differ both in the timing and rate of moult [30], giant petrels provide a powerful system to look at hormonal correlates of moult. By the time of hatching, giant petrels have begun moult, which continues throughout the rest of the breeding season, and both species fledge their chicks and out-migrate at the same time at the breeding season’s end, despite that Southern giant petrels begin breeding/moulting two months later than the Northern species [30]. Given the strong associations and empirically tested relationships between moult and both prolactin [9,15] and corticosterone [51],

and between incubation behaviour and prolactin [2], we examined seasonal profiles of prolactin and corticosterone secretion and moult scores during the breeding–moult overlap. The widespread (though not universal [18]) role of prolactin in incubation behaviour led us to predict that increasing prolactin would reveal a dissociation from moult in male Southern giant petrels, which, unlike the other species and sexes, begin moult early during incubation. In contrast, we predicted that in female Southern and both sexes of Northern giant petrels, which begin moulting towards the end of incubation, decreasing prolactin would herald the start of moult, as observed in the majority of birds in which prolactin–moult dynamics have been investigated. With respect to corticosterone, we predicted that the relatively high availability of food resources during the breeding season would make an up-regulation of corticosterone to facilitate increased foraging activity unnecessary. Therefore, we did not predict that plasma corticosterone would show seasonal up-regulation. Rather, we predicted that plasma corticosterone would be maintained at a fairly low, baseline, level and without a direct association with moult.

At the end of the breeding season before giant petrels depart the breeding colony, we also compare hormonal patterns to test predictions regarding the successful maintenance of both breeding and moult, especially as prolactin and corticosterone can both be involved in breeding failure [2,3,6,22]. For example, failed breeders should have lower prolactin and more advanced moult relative to birds still actively engaged in chick rearing. Therefore, we also compared relationships between prolactin, corticosterone, and moult in failed and active breeders to understand how these dynamics change when birds are released from the constraints of parenthood.

2. Material and methods

2.1. Field collection

Data were collected from Northern and Southern giant petrels breeding on Bird Island, South Georgia (54°00’S, 38°02’W) during the austral summer of 2008–2009. Northern giant petrels lay in mid September–mid October, chicks hatch in mid November–mid December, and fledge in mid March–early April. Southern giant petrels lay on average about 6 weeks later, in November, and chicks hatch in January and fledge in May (see [31]), and British Antarctic Survey unpublished data). The duration of the initial guard phase before the chick is first left alone is considerably longer in northern than southern giant petrels (30 vs. 16 days; see [31]). Sex of adult giant petrels can be determined reliably in the field based on bill dimensions [31], and all individuals in this study were part of the long-term population monitoring programme. A maximum of twenty males and 20 females of each species were sampled at four different times throughout the breeding season: after laying, before hatch, after hatch, and late in chick-rearing. This sequence spanned a 6 month period from October 2008 to April 2009. Only one bird was sampled from each nest, and no birds were subsequently re-sampled (e.g. we did not serially sample birds). Failed and successfully breeding petrels were also sampled during the last sampling period (late chick-rearing), just prior to dates of chick-fledging and adult out-migration. Dates of breeding failure for these late-season petrels were determined from weekly nest visits as part of the routine giant petrel monitoring program at Bird Island. Failure varied from 63 to 147 days prior to dates of sampling.

At most sampling periods, birds were approached at the nest. The exception was during late-chick rearing when active breeders (identified from the unique alphanumeric code on their plastic leg bands) are more likely found in small groups in open grassy areas

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