

# 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

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 corti-

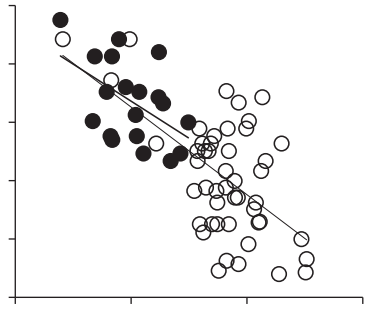
in the general vicinity of their nests. Upon capture, blood samples (2.0 ml) were collected from the tarsal vein using pre-heparinized syringes with 25 gauge needles. Blood was transferred to heparinized 2.5-mL Eppendorf vials, and from each a small sub-sample was removed with a micro-haematocrit tube and centrifuged for 5 min. at 10,000 g. The remaining blood was then centrifuged for 5 min at 10,000 g and plasma transferred to labelled 0.6-mL vials for storage at 20 °C until analysis. In nearly all cases (299 of 302), blood was collected in less than 3 min, which is necessary for interpreting baseline corticosterone levels [50]. Bill length and minimum depth, and tarsus length, were measured to the nearest 1.0 mm with calipers. Mass was measured to the nearest 10.0 g with Pesola spring scales. Mass-corrected primary feather moult was scored using the method outlined by [11]. To compare the progression of moult to a previous study of giant petrels on Bird Island, moult was also scored using the method outlined in [30]. Birds were then released with a dab of red paint on their breasts to ensure that they were not recaptured or disturbed on subsequent sampling dates. We did not make detailed notes on the effects of handling on subsequent chick egg/survival as the birds that we sampled were outside the designated area for giant petrel monitoring at Bird Island.

## 2.2. Hormonal assays

Prolactin was assayed in duplicate 20  $\mu$ l plasma samples in a recombinant-derived starling prolactin assay [5]. The sensitivity of the assay was 1.0 ng ml<sup>-1</sup>, and 50% displacement was obtained with 12.1 ng ml<sup>-1</sup>. All samples were measured in a single assay and the intra-assay coefficient of variation was 6.5%. For some samples, an extra 10  $\mu$ l was measured to ensure parallelism (Fig. 1). Corticosterone was determined by double antibody radioimmunoassay (<sup>125</sup>I-RIA, MP Biomedicals, 07-120103) with modifications validated for several avian species [42,54,57]. The assay detection limit was 3.13 pg corticosterone per tube (i.e. the lowest corticosterone standard, 12.5 ng ml<sup>-1</sup>, using a 50  $\mu$ l assay volume). The low corticosterone control and a consistent native plasma sample were analysed in each assay to determine an inter-assay coefficient of variation (5.10%). Intra-assay coefficient of variation

was 8.79% for the Northern giant petrels and 10.71% for the Southern giant petrels. Serially diluted native plasma samples were parallel to the corticosterone standard curve (coefficients of variation for final concentrations were 9.94% for Northern giant petrels (N = 3) and 7.48% for Southern giant petrels (





though these birds maintained parental care. These giant petrels therefore appear to have evolved behavioural or ecological means for avoiding any deleterious effects that low prolactin levels might exact on parental care, which we will discuss in greater detail below. However, we do not know the levels at which prolactin were maintained in the non-breeding birds at this stage of the season; it is possible that the breeding birds still had relatively higher levels than non-breeding birds, which would indicate a continued role of prolactin in parental care. In contrast, male Southern giant petrels initiated moult at a time when prolactin and corticosterone were both increasing, which stands as a rare exception among the majority of birds for which a decrease from seasonal prolactin peaks seems required for the initiation of moult [9]. This suggests that in male Southern giant petrels moult must be regulated by some alternate physiological pathway (e.g. the thyroid hormones [46], but see [9]) so as to avoid the negative effects of low prolactin on incubation behaviour when moult starts very early in reproduction. Indeed, the pattern of increasing prolactin in male Southern giant petrels conforms to many descriptive and experimental studies which show a positive link between prolactin and incubation behaviour [2].

As noted, with the exception of male Southern giant petrels, patterns of prolactin secretion and moult conformed to those observed in other species [9]: moult was initiated only once prolactin began decreasing from seasonal peaks, and for the Northern giant petrels and female Southern giant petrels, this decrease occurred when their eggs began hatching. What is interesting is that this decrease preceded a major shift in parental behaviour, after which

this trade-off via suppression of prolactin [3]. Our data clearly show that the loss of chicks allowed parent birds to shift from investment in parental care towards self-maintenance by directing time and resources to moult. In both male and female Southern giant petrels, a rapid down-regulation of prolactin was correlated with an accelerated rate of moult, and this is evident in Figs. 3 and 4 which show a significant inverse relationship between prolactin and moult among failed and successful individuals in both

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