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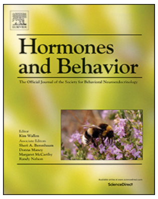

Sex- and breeding stage-specific hormonal stress response of seabird parents

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ABSTRACT

Changes in corticosterone (CORT) and prolactin (PRL) levels are thought to provide complementary information on parental decisions in birds in the context of stressful situations. However, these endocrine mechanisms have yet to be fully elucidated, appearing to vary among avian species without any clear pattern. Here, we examined CORT and PRL stress responses in a small Arctic seabird, the little auk (*Alle alle*). We analysed the levels of these hormones (baseline, and stress response, i.e. the change in the baseline in response to stress) with respect to the breeding phase (mid incubation and mid chick rearing) and the sex of the birds. Baseline CORT concentrations were similar during both breeding phases but baseline PRL levels were higher during incubation than chick rearing. The CORT and PRL stress responses were stronger during incubation than chick rearing (although with respect to CORT the effect was only marginally significant). There were also some sex-specific baseline levels and stress responses for both hormones (during the incubation period males compared to females exhibited higher CORT stress response and lower baseline PRL; during the chick rearing period males exhibited higher PRL stress response). Our results suggest that in the case of the little auk, both the incubation and the chick rearing periods may represent similar levels of physiological stress. However, the birds may be more sensitive to stress during incubation than during chick rearing, possibly because of inter-phase differences in predation pressure. The sex differences suggest differential exposure of males and females to stressors.

1. Introduction

Endocrine stress response is one possible mechanism regulating avian reproductive effort. Potentially deleterious stressors experienced by the parents, e.g. predators, extreme weather events, food shortages, activate neuro-hormonal pathways that change their behaviour (Wingfield and Sapolsky, 2003). The most important of these pathways involves activation of the hypothalamic–pituitary–adrenal axis (HPA), which leads to rapid and dramatic increase in the circulating level of corticosterone (CORT). According to the "emergency life history-stage" hypothesis, a sharp increase in the CORT level redirects resources away from activities inessential at a given moment, such as parental care, towards the immediate survival of the parent (Landys et al., 2006; Wingfield et al., 1998). When the stressor disappears, the CORT level returns to a low concentration and reproductive activities are resumed. But, when the stressor is chronic, CORT levels remain high, and this leads to a dramatic reduction in parental care, including brood abandonment (e.g. Ouyang et al., 2012).

The CORT stress response is a well understood mechanism regulating parental investment. But there is another hormone, that could also play a part in regulating reproductive effort as it affects parental activities directly: this is prolactin (PRL) (Angelier and Chastel, 2009; Chastel et al., 2005). CORT and PRL levels often appear to provide complementary information regarding parental decisions in the context of stressful situations: CORT is primarily related to the parents' survival, while PRL is associated with benefits to the offspring (Angelier et al., 2009, 2016; Angelier and Chastel, 2009; Chastel et al., 2005; Heidinger et al., 2006). Although the pattern of changes in baseline PRL levels over the breeding season differs among species, depending on the offspring developmental mode, PRL secretion is dramatically accentuated in all species when individuals enter the parental phase (Angelier et al., 2016; Dawson and Goldsmith, 1983). Some experimental studies have clearly demonstrated casual role of PRL in post-hatching care (Smiley and Adkins-Regan, 2018; Wang and Buntin, 1999). Be that as it may, the PRL stress response is still not well understood. A growing, though still limited, body of data for birds suggests that the PRL concentration in breeders decreases during stressful events (Angelier et al., 2016; Angelier and Chastel, 2009; Chastel et al., 2005; Opel and Proudman, 1986; Sharp et al., 1989). If PRL level drops below a certain threshold, as a result of acute or chronic stress, parental activities cease (Angelier

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et al., 2016; Angelier and Chastel, 2009; Chastel et al., 2005). The direction and magnitude of this response may, however, be stage- or concentration-dependent, because the PRL level has also been reported to remain stable or even increase in response to acute stress, with no effect on parental performance (reviewed in Angelier et al., 2016).

Numerous studies have demonstrated that the effect of a stressor on endocrine response is not always the same, and depends on current circumstances. According to the "brood value hypothesis" (reviewed in Bókony et al., 2009), baseline CORT and PRL levels and hormonal stress response should vary depending on the relative importance of the current reproductive effort. If the value of this is relatively high, the baseline level of CORT should be reduced, and that of PRL elevated, and the stress response of both hormones should be attenuated; this ensures that the current breeding attempt is not compromised (Bókony et al., 2009). Consequently, parents in short-lived birds, which have just a small number of reproductive attempts at their disposal, are expected to have higher CORT and PRL baseline concentrations, and to mitigate the stress response of both hormones, all in order to maximize reproduction during the current breeding attempt. In contrast, parents in long-lived, iteroparous species (i.e. with multiple reproductive cycles over the course of the lifetime), are expected to exhibit the opposite pattern of baseline levels of both hormones and to sustain hormonal stress responses at a high level, thus preventing their own survival from being jeopardized (Angelier et al., 2016; Angelier and Chastel, 2009; Bókony et al., 2009; Drent and Daan, 1980). This is because the lifetime reproductive success of long-lived species is primarily a function of adult survival rather than of seasonal fecundity (Williams, 1966). Following the same line of reasoning, the brood value is believed to increase as the breeding season progresses. When opportunities for replacement breeding in the current season are limited, the importance of current reproduction increases considerably (e.g. Breuner et al., 2003; O'Reilly and Wingfield, 2001; Silverin et al., 1997). Hence, the hormonal stress response is expected to attenuate with the progress of the breeding season (Bókony et al., 2009). The result of the few studies to have investigated the hormonal stress response over the breeding season are contradictory: on the one hand, they support the brood value hypothesis in that they reveal a lower stress response in the late phase of breeding compared to earlier phases (e.g. the grey-face-petrel *Pterodroma macroptera gouldi*; Adams et al., 2005), while on the other they do not support it, demonstrating no differences in hormonal levels between the breeding phases (e.g. the Manx shearwater *Puffinus puffinus*; Riou et al., 2010). Finally, the brood value and hormonal levels may be differently modulated in males and females, depending on the amount of parental care provided by each sex. It has been demonstrated for several species that the sex investing more in offspring care exhibits higher baseline CORT and PRL levels, and a weaker hormonal stress response (Holberton and Wingfield, 2003; O'Reilly and Wingfield, 2001; Wingfield et al., 1995).

In this study we examined CORT and PRL stress response in the little auk (or dovekie, *Alle alle*), a small pelagic seabird, breeding exclusively in the high Arctic. Being a high-latitude species, the little auk is expected to exhibit a weak stress response when breeding, as it is adapted to the extreme, stressful weather events that are relatively frequent in the polar zone (Breuner et al., 2003; O'Reilly and Wingfield, 2001; Silverin et al., 1997, but see also Bókony et al., 2009). Moreover, because of the little auk's long nesting period and the short time-window of the Arctic summer with favorable environmental conditions (both ca 2 months), only one brood is completed annually, and opportunities for replacement breeding are extremely limited. Presumably, only breeders re-nesting early in the season stand any chance of successfully rearing a replacement brood, even though their chicks are usually in a worse body condition than those hatched earlier in the year (Jakubas and Wojczulanis-Jakubas, 2013). In such time-constrained breeding circumstances, selection is expected to attenuate the breeders' hormonal stress responses. On the other hand, the little auk is a typical seabird: it is long-lived, with a life-span of at least ten - twenty years, (own unpublished data), and a prolonged phase of bi-parental care for a single chick. Given these life-history traits, little auk parents are expected to respond strongly to stressful situations, prioritizing their self-maintenance and survival over the wellbeing of their offspring. Contrasting expectations regarding the magnitude of the stress response in the little auk make the species particularly interesting, especially that avian stress responses have been little studied in high-latitude seabirds.

We examined CORT and PRL stress response in the little auk with respect to the breeding phase (mid incubation and mid chick rearing) and sex. Basically, we focused on changes in the levels of these hormones in response to stress; but in order to obtain a fuller picture, we also analysed their baseline levels, and the relationship between the baseline and stress response levels of both. Given the time-constraints imposed by the Arctic summer (Moe et al., 2009), we assumed that the brood value did not change for little auk parents across the breeding phases. Thus, we expected no differences in hormonal stress responses between the mid-incubation and mid-chick rearing periods; neither did we expect any differences in CORT baseline levels. Although the parental care provided during the two breeding phases takes fundamentally different forms, previous inter-phases comparisons of baseline CORT levels in the little auk did not yield significant differences (Wojczulanis-Jakubas et al., 2015). We did expect differences in baseline PRL levels, however, with higher values during mid-incubation than mid-chick rearing. This is because baseline PRL generally increases rapidly with the onset of incubation in semi-precocial species like the little auk and remains at stable high level throughout the incubation period (Angelier et al., 2016; Massaro et al., 2007; Vleck et al., 2000). After hatching, it drops slightly, thereafter decreasing gradually (Angelier et al., 2016). The baseline PRL level in the mid-chick rearing period in the little auk should thus be much lower than during the mid-incubation period. This is consistent with previous inter-phase comparisons of baseline PRL levels in this species (Wojczulanis-Jakubas et al., 2015). With regard to sex, we did not expect any differences in hormone levels and stress responses during the two breeding phases between males and females they make similar contributions to parental care during both incubation and chick rearing (Harding et al., 2004; Wojczulanis-Jakubas et al., 2009). There are no apparent differences between the parents in the amounts of time they spend at the nest during the incubation period (Wojczulanis-Jakubas et al., 2009). Moreover, for most of the chick rearing phase, both parents brood and feed their offspring with a similar frequency (Wojczulanis-Jakubas et al., 2012). The only differences in parental care occur at the end of the chick rearing phase, when the female ceases feeding but the male continues to care for the chick and escorts it during its departure from the colony. For this reason, little auk males have been hypothesized to be less sensitive to stressors than females: escorting the chick during its first flight to sea is expected to be a stressful event because of the greater predation pressure in that period (Wojczulanis-Jakubas et al., 2005). However, a study comparing baseline and stress-induced hormone concentrations between the two sexes during the chick rearing period did not reveal significant differences (Wojczulanis-Jakubas et al., 2013).

2. Materials and methods

2.1. Fieldwork

We carried out the study in a large little auk breeding colony on the Ariekammen slopes in Hornsund (SW Spitsbergen, Norway; 77°00′ N, 15°33′ E). We considered only active breeders and used two capture methods, both of which effectively minimized the handling time to < 3 min (crucial for the standardized capture-restraint protocol (Wingfield et al., 1994, see below). During the incubation period (season 2014), we captured the birds by hand while they were incubating on the nest. The breeding status of the incubating birds was self-evident, and the individuals were sampled on day 9–12 of the