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Linking sex differences in corticosterone with individual reproductive behaviour and hatch success in two species of uniparental shorebirds

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ABSTRACT

In birds, corticosterone (CORT) appears to facilitate reproductive activity because baseline and stress-induced CORT levels are elevated in breeding individuals compared with other times of the year. In particular, CORT is lower in the sex providing most of the parental care (i.e., incubation), which could be an important adaptation to tolerate stressors that result in abandoning reproduction. Therefore, one explanation for sex differences in CORT is that lower levels are favoured during the incubation/parental phase of reproduction. Using two species of uniparental shorebird – polyandrous red phalaropes (*Phalaropus fulicarius*) and polygynous white-rumped sandpipers (*Calidris fuscicollis*) – we predicted that the incubating sex would have lower baseline and stress-induced CORT, and incubating individuals with lower CORT would more effectively defend nests against a simulated intrusion, would return more quickly afterwards, and would ultimately have higher hatch success. We found that phalaropes followed the predicted pattern: incubating individuals (males) had lower baseline and stress-induced CORT than females but for baseline CORT these differences existed prior to males commencing incubation. Incubating male phalaropes with lower baseline and stress-induced CORT returned to incubate more quickly after a disturbance and there was non-significant tendency for baseline CORT to be lower in successful nests. In sandpipers, we observed no sex differences and no significant relationships between individual CORT levels and nest defence behaviours or hatch success. Our results demonstrate that in phalaropes at least, selection favours lower baseline and stress-induced CORT during the nesting period. These results can explain sex differences in stress-induced levels of CORT, however sex differences in baseline CORT were present prior to incubation.

1. Introduction

Glucocorticoids, such as corticosterone (CORT) in birds, mediate the behavioural and physiological responses to both unpredictable short-term (i.e., acute stressors) and predictable long-term (i.e., life history stages) challenges (Landys et al., 2006). As such, individual differences in baseline hormone expression during normal physiological conditions and acute response to stress are thought to be subject to strong selection (Breuner et al., 2008; Bonier et al., 2009).

At seasonal baseline levels, increases in CORT reflect energetic demands (Bonier et al., 2009). Elevated CORT liberates energy stores via gluconeogenesis (Remage-Healey and Romero, 2001) and modifies behaviour such as feeding rate (Wingfield et al., 1990), aggression (Kitaysky et al., 2003) and/or locomotory activity (Wingfield et al., 1998). Following exposure to an acute stressor, CORT increases rapidly from baseline levels to initiate behavioural and physiological changes that are thought to promote current survival (Sapolsky et al., 2000; Breuner et al., 2008); one such effect is to abandon parental duties (e.g., Silverin, 1986). Consequently, both baseline (Bonier et al., 2009) and acute (Breuner et al., 2008) CORT levels are expected to be linked to fitness.

CORT levels typically vary seasonally (Breuner and Orchinik, 2001) suggesting that it is adaptively regulated in response to different life history stages, such as breeding. Adrenal activity is upregulated during the breeding season (Romero and Wingfield, 1998) and as a consequence, breeding individuals tend to have a higher baseline and acute CORT response to stress (hereafter termed 'stress-induced CORT') than at other times of the year or when compared with non-breeding individuals (Astheimer et al., 1994; Romero and Wingfield, 1998; Cornelius et al., 2012).

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Sex differences in CORT are thought to reflect sex-role differences and facilitate sex-specific reproductive behaviours. Among breeding birds, males often have higher baseline and stress-induced CORT than females in species that display sexually dimorphic reproductive behaviours (Astheimer et al., 1994; Holberton and Wingfield, 2003; Meddle et al., 2003). In tree (*Spizella arborea*) and white-crowned sparrows (*Zonotrichia leucophrys gambelii*), males have higher stress-induced CORT during the preparental stage when behaviours differ between the sexes, but males were similar to females during the parental stage when both sexes fed the young (Holberton and Wingfield, 2003). These observations have led to the notion that lower stress-induced CORT in incubating birds functions to prevent nest abandonment by the incubating sex during stressful conditions (O'Reilly and Wingfield, 2001). In support of this, the sex providing more parental care has lower stress-induced CORT (males in polyandrous species and females in polygynous species) and there is no apparent sex difference when both sexes contribute evenly (O'Reilly and Wingfield, 2001; but see O'Reilly and Wingfield, 2003). Furthermore, females have weaker CORT responses in species where they provide more parental care possibly due to the value of the brood as a function of renesting opportunity during shorter breeding seasons (Bókony et al., 2009).

Because of these observations, sex differences in CORT are thought to be the result of selection for reduced CORT levels in parental birds. In support of this, breeding adult birds with naturally high levels of baseline CORT have higher abandonment rates (Groscolas et al., 2008; Spée et al., 2010), as do birds with artificially elevated CORT (Silverin, 1986; Angelier et al., 2009a; Spée et al., 2011). Yet, a natural, acute stress response may be an important part of mounting a strong and successful nest defence. Nest defence is positively related to reproductive success (Garcia, 2003; Goławski and Mitrus, 2008), and a strong nest defence is especially important for ground nesting birds where predation accounts for a significant proportion of failed nest attempts and abandonment is otherwise infrequent (Smith and Wilson, 2010). Acute glucocorticoid exposure increases aggression in a variety of animals (Wingfield and Silverin, 1986; Hayden-Hixon and Ferris, 1991; DeNardo and Licht, 1993; Haller et al., 1997; Kitaysky et al., 2003) and so the ability to mount a defence of the nest could be positively related to the magnitude of the adrenocortical response (i.e., stress-induced CORT). However, much of the work to date has been focussed on implants that cause 'short-term' effects that last hours to days, rather than an actual measure of the acute stress response.

As a means of explaining sex differences in CORT levels, we sought to link individual behaviour and hatch success with baseline and stress-induced CORT levels in two species of uniparental shorebird: polygynous white-rumped sandpipers (*Calidris fuscicollis*) and polyandrous red phalaropes (*Phalaropus fulicarius*). In polygynous sandpipers, females are the sole incubators but in phalaropes males incubate and females do not. We outline three predictions addressed by this study. Prediction 1) If baseline and stress-induced CORT levels are attenuated to facilitate incubation and prevent nest abandonment, we predict that the incubating sex (female sandpipers and male phalaropes) should have lower levels than the non-incubating sex. Prediction 2) Because CORT is expected to be related to defensive and nest guarding behaviour, we predict that individual incubators with low baseline and stress-induced CORT levels should flush less readily from nests, perform stronger nest defence displays and return more quickly to the nest following a disturbance. Prediction 3) Individuals with lower CORT levels will have higher hatch success.

2. Materials and methods

2.1. Field site and species

We examined white-rumped sandpipers (*C. fuscicollis*) and red phalaropes (*P. fulicarius*) (hereafter referred to as sandpipers and phalaropes) at East Bay Migratory Bird Sanctuary, Nunavut, Canada (N63 59 13.5 W81 41 48.3) during June–July 2008–2010. These two species are small-bodied ground nesting shorebirds. At our site, mean male and female body mass of sandpipers is 43.7 g and 42.6 g respectively, and for phalaropes 49.4 g and 57.1 g. During incubation, both species rely on crypsis to avoid nest predation until a predator approaches too closely. Once the predator has approached too closely, the two species employ slightly different tactics: sandpipers undertake rather convincing distraction displays (e.g., 'broken-wing display' or 'rodent run') with relatively few individuals leaving the nest site without producing any display. By contrast, phalaropes frequently flush without producing a display, or less frequently, perform a milder form of a broken-wing display (pers. obs.). The nesting habitats of the two species overlap completely at our field site with most individuals of both species nesting in upland *Dryas* hummocks and sedge meadows; the landscape if predominantly flat with vegetation less than 15 cm in height.

2.2. Trapping and blood collection

We trapped male sandpipers, and both male (prior to incubation) and female phalaropes during the courtship period; we were unable to capture adequate numbers of female sandpipers at this time, and most of those we did capture were carrying eggs and so considered in a physiologically distinct stage. We termed pre-incubation birds 'courtship'. We used the presence of a brood patch to determine whether male phalaropes were incubating. We caught courtship birds by stalking them while they were feeding or displaying/defending territories using a Super Talon net gun (Fly Dragon Technology Co., Ltd) (Edwards and Gilchrist, 2011). We trapped incubating female sandpipers and incubating male phalaropes using either bownets or Fundy Jerk Traps placed on the nest. These traps allow birds to come and go from the nest and are manually triggered so can be placed for longer periods of time without interrupting feeding and incubation intervals.

We caught a total of 62 white-rumped sandpipers (45 incubating females and 17 courtship males) and 112 phalaropes (38 courtship females, 37 courtship males and 36 incubating males). Both species are polygamous and courtship activities of male sandpipers and female phalaropes extend into the incubation period. Nevertheless, courtship activity declines making courtship birds more scarce and incubating birds more abundant as the season progresses. Additionally, we could not confirm that birds trapped later in the season were not in an ambiguous or confounding physiological state such as could be expected by including failed or post-breeding individuals in the study. For these reasons, trapping periods did not perfectly overlap for some stages. We trapped male sandpipers from 156 to 173 Julian Day (JD) (mean 164) and incubating females from 172 to 204 JD (mean 186). In phalaropes, females were trapped from 161 to 188 JD (mean 171), courtship males 160 to 188 JD (mean 172) and incubating males from 171 to 201 JD (mean 189).

A stopwatch was started immediately when the trap was deployed (either the net gun was shot or the nest trap triggered) and a 'baseline' blood sample was taken within 4 min, but usually in less than 3 min (90% of samples; mean baseline bleed time: 2.3 min ± 0.8 min). The bird was measured, banded and subjected to a standard stress protocol (Wingfield et al., 1992). Blood was collected in heparinised capillary tubes, and volumes drawn were typically between 50 and 100 μL per bleed as blood samples were used as part of a larger study. After 30 min (mean stress-induced bleed time after first bleed: 30.4 min ± 1.7 min) a second blood sample was taken from the other wing to reflect the 'stress-induced' value for CORT (hereafter, stress-induced CORT). There was no difference between trapping methods in the length of time it took to collect a blood sample. Blood samples were kept cool for up to 6 h at which point they were centrifuged and the plasma frozen at −20 °C until