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Context dependency of baseline glucocorticoids as indicators of individual quality in a capital breeder

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ABSTRACT

Identifying markers of individual quality is a central goal of life-history theory and conservation biology. The 'corticosterone (CORT)-fitness hypothesis' postulates that low fitness signals impaired ability to cope with the environment, resulting in elevated baseline CORT levels. CORT can, however, be negatively, positively or neutrally related to fitness, depending on the context. In order to clarify this controversial issue, we elucidate the utility of using baseline CORT as a correlate of individual fitness in incubating female eiders across variable environments. An increase in serum CORT with decreasing body condition was evident in older, more experienced breeders, while increased clutch mass was associated with elevated serum CORT in females breeding late in the season. For faecal CORT, the expected negative association with body condition was observed only in early breeders. We found a strong increase in faecal CORT with increasing baseline body temperature, indicating the utility of body temperature as a complementary stress indicator. Females in good body condition had a lower baseline body temperature, but this effect was only observed on open islands, a harsher breeding habitat less buffered against weather variability. Females with higher reproductive investment also maintained a lower baseline body temperature. Nest success strongly decreased with increasing serum and faecal CORT concentrations, and individual stress hormone and body temperature profiles were repeatable over years. Although our data support the tenet that baseline CORT is negatively related to fitness, the complex context-dependent effects call for cautious interpretation of relationships between stress physiology and phenotypic quality.

1. Introduction

Identifying markers that quantify individual performance in the face of environmental challenges is a central goal of life-history theory and conservation biology (e.g., Cockrem, 2005). Physiological, especially endocrine, mechanisms may serve as such markers, and these mechanisms also show promise in mediating life-history trade-offs between survival and reproduction (reviewed in Crespi et al., 2013). Glucocorticoid (GC) hormones, such as corticosterone (CORT), may play a particularly important role in this regard, as they regulate the allotment of energy between reproduction and survival (Bókony et al., 2009). Furthermore, as GC concentrations show high individual variation (e.g., Cockrem and Silverin, 2002) that is partly heritable (Evans et al., 2006), and affects survival and reproductive performance (e.g., Romero and Wikelski, 2001), they are likely to be a target of selection.

The 'corticosterone-fitness hypothesis' postulates that, all other things being equal, individuals with low predicted reproductive output or survival should exhibit elevated baseline CORT levels as a result of their impaired ability to cope with their environment (Bonier et al., 2009a). Although backed up by a fair amount of empirical support in the literature (e.g., Sheriff et al., 2009), it is becoming increasingly clear that this hypothesis is overly simplistic because, in reality, all other things are seldom equal and CORT can in fact be negatively, positively or neutrally related to fitness, depending on the context (Crespi et al., 2013). For example, the relationship between GCs and fitness may change within individuals in different phases of their annual cycle, particularly during the transition from non-breeding to a reproductive state (Bonier et al., 2009b; Ouyang et al., 2011). Thus, heavy investment in reproduction may concomitantly increase both reproductive success (i.e., fitness) and CORT levels, which forms the basic tenet of the

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'CORT-adaptation hypothesis' (Bonier et al., 2009a). Indeed, there is growing evidence that elevated GC levels may facilitate rather than interfere with reproductive investment (e.g., Crossin et al., 2012), spurring controversy as to the interpretation of the relationship between stress and fitness on the individual level (Bonier et al., 2010; Dingemanse et al., 2010).

Our current understanding of stress-response mechanisms is also hampered by a failure to account for other intrinsic and external factors affecting both life histories and the secretion of GCs by the hypothalamic–pituitary–adrenal (HPA) axis (Crespi et al., 2013). The relationship between CORT and fitness should preferably be measured at different times (i.e., in multiple reproductive seasons) and/or across different habitats consistently differing in their perceived harshness. So far this has mainly been attempted with across-species comparisons between distinct environmental types (e.g., Wada et al., 2006; Hau et al., 2010), whereas comparisons within a species are largely lacking (Crespi et al., 2013). This is unfortunate, because the relationship between individual quality and stress resistance is only observable at the within-species level, once potential interactions between individual quality and the environment are taken into account (D'Alba et al., 2011). For example, the ability to cope with stressors may decline with decreasing individual quality, but this relationship may only be evident in harsh environments (Charmantier and Garant, 2005; Descamps et al., 2009; Robert et al., 2012).

Recently, Crespi et al. (2013) called for more longitudinal studies measuring effects of GCs on multiple life-history traits in different environmental contexts. To heed this call we here shed light on the utility of baseline CORT as a correlate of individual fitness across variable environments. We do this in incubating eider females (*Somateria mollissima*), which are especially suited for elucidating potential connections between individual quality, CORT and fitness because they are long-lived capital breeders which rely almost entirely on bodily reserves during incubation, losing up to 40% of their pre-laying body weight (e.g., Parker and Holm, 1990). Individual differences in body condition are likely to be pronounced during incubation because there is substantial variation in both energy reserves at incubation onset and weight loss during incubation (Hanssen et al., 2002; Öst et al., 2008b), and females cannot compensate for such differences due to complete breeding anorexia. Previous studies indicate that breeding success is largely determined by body condition, breeding experience and timing of breeding (Lehikoinen et al., 2010; Öst and Steele, 2010), wherefore these traits can be regarded as correlates of individual quality in eiders (Jaatinen and Öst, 2011). The fact that females do not replenish their energy reserves during incubation facilitates direct comparison of CORT secretion and fitness between individuals nesting in vicinity of one another. Furthermore, eiders breed in two contrasting habitat types, open and forested islands, of which open islands are more exposed to weather extremes (Kilpi and Lindström, 1997) and predation risk (Ekroos et al., 2012).

We first examined links between individual quality and baseline CORT levels in blood and faeces, using multiple correlates of individual quality (breeding experience, body condition, hatch date, clutch mass). Because high CORT levels may be associated with a rise in body temperature (e.g., Cabanac and Guillemette, 2001), we also included female baseline body temperature during incubation in the analyses. We predicted that elevated baseline CORT should be found in individuals of low quality. Next, we explored whether the relationship between baseline body temperature) and individual quality was modulated in the two habitats contrasting in their degree of thermal protection. We predicted that low-quality individuals would be disproportionately affected by a challenging thermal environment, reflected in concomitant changes in their baseline body temperature. Third, we tested whether baseline CORT levels were repeatable, a prerequisite for linking baseline CORT to a fitness component (Bonier et al., 2009a; Angelier et al., 2010), and we also assessed whether baseline body temperature was repeatable within individuals over years. Finally, we determined the relationship between CORT and fitness, in terms of nest success, controlling for breeding experience, body condition and hatch date. Under the CORT-fitness hypothesis, we expected a negative correlation between baseline CORT and reproductive success, and we further expected the relationship to be consistent for both of our CORT measures, since different stress measures should positively co-vary (Crespi et al., 2013).

2. Methods

2.1. Field methods

This study was conducted at Tvärminne (59°50′N, 23°15′E), western Gulf of Finland, in 2009–2011. We also utilized data on faecal CORT concentrations from 2008 in the corresponding repeatability analysis to improve statistical power. In this study area, females nest on small open islands or on larger forested islands. Females were captured during nesting by using hand nets. Upon capture, females were weighed, measured for structural size (length of the radius-ulna) and ringed with a standard metal ring. We calculated the number of years since the bird was first ringed and used this as a minimum estimate of years of maternal experience (Öst et al., 2008a; Öst and Steele, 2010; Jaatinen and Öst, 2011). This is a reasonably accurate indicator of breeding experience because females are highly philopatric to their breeding islands (Öst et al., 2011), more than half of the successfully breeding females on our study islands are trapped annually (Jaatinen and Öst, 2011), and annual trapping effort has been similar since 1996. The incubation stage was estimated using an egg flotation test, which gives an estimate of how long a female has incubated her eggs (Kilpi and Lindström, 1997). Female eiders included in the current study incubated an average (±SD) of 27.21 (±2.18, $n = 286$) days, and because not all females managed to hatch their clutches successfully, hatch date was therefore calculated by adding 27 days to the date of the flotation test and subtracting the number of days the female had incubated. Clutch masses were made comparable between females by measuring total clutch mass and correcting for incubation stage, as eggs become lighter as the incubation progresses. This was done by calculating the raw residuals (in grams) from a linear regression of clutch mass on incubation stage. Clutch mass is a good measurement of reproductive investment in this capital breeding species, as all eggs are produced from stored reserves (Parker and Holm, 1990), and because the frequency of conspecific brood parasitism is low in this population (ca. 6% of eggs are of non-natal origin; Waldeck et al., 2004).

Trapping took place predominantly during the end of the incubation period in late May to minimize nest desertion. The time spent on each island during a bout of female capture was held to a minimum to decrease disturbance. During each capturing session on an island, we recorded the time elapsed between the first female being either flushed or caught off her nest and the capture of each female. This variable (hereafter capture timing; average [±SD] = 29.88 [± 26.78] min, $n = 535$) was used to control for any rise in baseline CORT levels due to females potentially seeing us capture other females at a distance. Potential researcher-induced nest desertion is largely restricted to the early phases of incubation, whereas the frequency of nest visits does not influence the probability of nest desertion, provided that the first visit is timed to the later phases of incubation (Bolduc and Guillemette, 2003). A detailed account of the ethics involved in female capture is