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Assessing baseline stress physiology as an integrator of environmental quality in a wild avian population: Implications for use as a conservation biomarker

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ABSTRACT

Stress hormones (i.e., glucocorticoids such as corticosterone and cortisol) have been widely proposed as biomarkers of habitat quality and disturbance. However, there is growing evidence that baseline glucocorticoid (GC) levels are highly context-dependent, potentially confounding their utility for inferring population-level disturbance depending on the life history stage and the duration, severity, and type of environmental change being measured. Determining which aspects of an organism's environment are consistently reflected by baseline GC levels is therefore of paramount importance to establishing how they may be best suited to conservation monitoring goals. We investigated the relationship between baseline GC levels and three extrinsic (food availability, inter-specific nest competition, intra-specific competition) and two intrinsic (reproductive investment, body condition) environmental contexts in breeding female tree swallows (*Tachycineta bicolor*) at two reproductive stages. We combined this with a manipulation of energetic demand (i.e., a decrease in foraging profitability) to determine whether baseline GCs reflect the extrinsic or intrinsic environment when females are faced with an unexpected disturbance. Baseline GC levels were not reflective of any environmental component in control females, regardless of reproductive stage. However, levels increased and were reflective of a decrease in body mass when females were challenged during the offspring provisioning period. Our findings suggest that baseline GCs may not always be indicative of the environmental contexts we associate with variation in habitat quality, particularly when individuals are operating within their expected energetic demand. In a conservation sense, baseline GCs may be more valuable in reflecting unexpected perturbations, which could limit their applicability as sensitive, predictive biomarkers across a diversity of systems.

1. Introduction

The ability to detect anthropogenic disturbances in wildlife populations is of paramount importance to monitoring and conservation management (Nichols and Williams, 2006). As traditional demographic measures are often labor-intensive and require extended time spans to detect population trends, many conservation biologists have begun to employ more sensitive, labile physiological measures to monitor the health and condition of wildlife systems of interest (Cooke et al., 2013; Seebacher and Franklin, 2012 and Wikelski and Cooke, 2006). The growing field of conservation physiology offers many potential traits spanning energetics, immune function, toxicology, reproductive biology and nutrition, each with their own optimal conditions for use and considerations for interpretation (Cooke et al., 2013). However, for a given physiological measure to be a sensitive biomarker, it must be reflective of the environmental changes that can influence condition, population health, and viability (Cooke and O'Connor, 2010). Glucocorticoids (i.e., cortisol, corticosterone) represent potential biomarkers due to their function in the maintenance of energetic balance (Landys et al., 2006), mediation of life history trade-offs (Crespi et al., 2013), and role in allowing individuals to respond behaviourally to perturbations in their environment (Wingfield, 2013).

Glucocorticoids (GCs) can be measured at baseline and stress-induced levels through blood samples (plasma or serum), and over more integrated time periods in feces and keratinized outer integuments such as hair and feathers (Sheriff et al., 2011). Baseline measures are appealing because they are obtained less invasively when compared with the handling protocol required to achieve stress-induced samples and although still more invasive than fecal collection, blood samples always allow GC levels to be tied unambiguously to individuals and time periods. Perhaps most importantly, baseline GCs have been theoretically viewed as integrators of an individual's internal and external environment (Fig. 1) due to their role in maintenance of energetic balance through the promotion of foraging and the mobilization of stored

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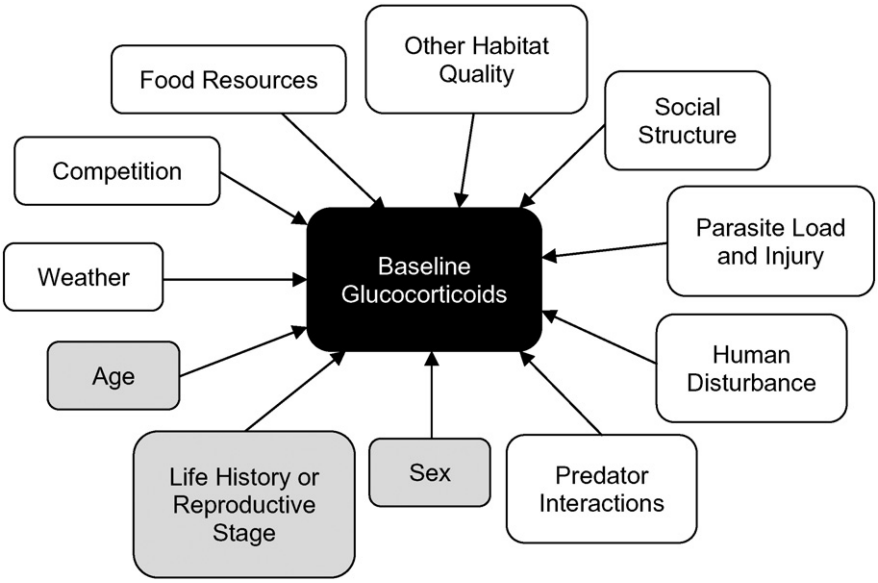

Fig. 1. Intrinsic (gray) and extrinsic (white) environmental variables expected to influence baseline glucocorticoid levels.

energy reserves (Dantzer et al., 2014; McEwen and Wingfield, 2010, and Shultz and Kitaysky, 2008). We would therefore expect an observable increase in baseline GC levels with any change in the environment that necessitates increased energetic expenditure or decreased access to food resources (i.e., increased energy expense or allostatic load; McEwen and Wingfield, 2010). Indeed, more energetically demanding life history stages are characterized by increased baseline GC levels (Romero, 2002), and on a finer temporal scale, more demanding stages of reproduction have been associated with higher baseline GC levels (e.g., Bonier et al., 2009; Reedy et al., 2014 and Rubenstein and Wikelski, 2005).

Baseline GCs have also been shown to be representative of a variety of conservation-relevant variables (Busch and Hayward, 2009) including vegetation cover (Bauer et al., 2013; Janin et al., 2012 and Stabach et al., 2015), parasite load (Bauer et al., 2013), urbanization (Bonier, 2012 and French et al., 2008), predation pressure (Clinchy et al., 2011), forestry practices (Leshyk et al., 2012), pollution (Nordstad et al., 2012), traffic intensity (Strasser and Heath, 2013), tourism (French et al., 2010) and food availability (Fokidis et al., 2012). However, whether and in which direction GC levels change has not been consistent despite the predominant assumption that any disturbance will lead to an increase in GC levels (Bonier et al., 2011; Dickens and Romero, 2013 and Madliger and Love, 2014, 2015). As a result, baseline GC levels may respond to environmental variation in a context-dependent manner that necessitates the careful consideration of underlying reproductive, demographic, or conditional parameters (Madliger and Love, 2014).

Investigating multiple aspects of environmental quality (both internal and external) may help to determine which components most sensitively correlate to GC levels. Unfortunately, few studies have investigated how multiple components of environmental quality may influence baseline GC levels simultaneously, particularly across gradients (Bauer et al., 2013; Grunst et al., 2014; Strasser and Heath, 2013 and Zhang et al., 2011). In addition, we currently have limited information on how baseline GCs may integrate environmental contexts differently depending on reproductive stage. This is particularly important given that timing of sampling could be highly relevant when considering GCs as physiological biomarkers since even short time periods (e.g., those separating different stages of reproduction) can have profound influences on underlying baseline GC levels (e.g., Pereyra and Wingfield, 2003; Kern et al., 2005; Goymann et al., 2006; Rector et al., 2012 and Williams et al., 2008). From a practical perspective, this type of information is necessary for conservation managers to determine whether certain time periods may be better-suited to the sampling of GCs, or whether contexts that vary within a population (e.g., reproductive status) could influence the ability of GCs to represent disturbances or environmental quality.

We combined three years of reproductive monitoring data, an experimental manipulation of energetic demand, and an assessment of multiple components of habitat quality to determine whether baseline GC levels represent a relevant biomarker of the intrinsic state and extrinsic environmental quality experienced by breeding female tree swallows (*Tachycineta bicolor*). Tree swallows are a member of the aerial insectivore guild which has been experiencing dramatic population declines in North America (Nebel et al., 2010); as a result, investigating how stress physiology relates to underlying variation in body condition and habitat quality can also contribute to our understanding of how future changes may influence this species and others in the guild. We specifically focused on two reproductive stages that differ in their parental energetic demand (Tatner and Bryant, 1993): incubation (lower demand) and offspring provisioning (higher demand). We chose environmental variables that represent major extrinsic and intrinsic factors that individuals of this species would experience during reproduction (Table 1), and that would therefore be expected to influence overall energetic management through changes in activity level or body reserves: 1) food availability; 2) inter-specific nest competition; 3) intra-specific nest competition; 4) reproductive investment (i.e., clutch size and brood mass); and 5) intrinsic state (i.e., body condition). We also experimentally increased energetic demand through feather clipping to test whether baseline GC levels are responsive to, and differentially influenced by, these environmental contexts when individuals are faced with an unexpected and prolonged disturbance while raising offspring (i.e., a decrease in foraging profitability and therefore the overall quality of their environment). Importantly, our manipulation forced individuals outside of preferred (optimal) investment decisions, but not past their capacity to successfully raise offspring. If baseline GCs are to be used as conservation-relevant biomarkers, we would predict that levels would be correlated with intrinsic and extrinsic environmental factors at both stages of reproduction. We also predicted that due to an increase in energetic demand (Tatner and Bryant, 1993), baseline GC levels would increase over the reproductive period, and levels of birds facing an unexpected decrease in environmental quality (feather clipping) would be elevated in comparison to control individuals.