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Diversity

The Need for a Predictive, Context-Dependent Approach to the Application of Stress Hormones in Conservation

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Introduction

Monitoring the impact of anthropogenic disturbance on species or populations of interest is an important goal of conservation (Van Dyke 2008). Because the effects of environmental alteration often manifest in an organism's physiology before changes can be detected at the population level, physiological measures can provide earlier detection of disturbances and greater predictive capacity than traditional demographic methods (Wikelski & Cooke 2006; Ellis et al. 2012). This mechanistic approach, known as conservation physiology, can also help determine which populations are most susceptible to disturbance, key periods when disturbances may be most detrimental, and whether management techniques are having positive effects (Carey 2005; Wikelski & Cooke 2006). Incorporating physiological biomarkers into population monitoring also provides the opportunity to interpret anthropogenic changes from the perspective of the organism rather than the researcher and thus improve our understanding of which conditions constitute a disturbance.

Glucocorticoids (GCs), often referred to as stress hormones, represent some of the most widely proposed physiological biomarkers (Cooke & O'Connor 2010). GCs (e.g., corticosterone and cortisol) act in 2 distinct and separately measurable ways as determined by their circulating concentration and the receptors to which they bind (Landys et al. 2006). GCs are best known for their role in enabling individuals to respond to unpredictable events such as extreme weather, predator interaction, or social conflict through the acute stress response (McEwen & Wingfield 2003). By increasing within minutes of an acute environmental challenge, GCs act to mobilize stored energy reserves, enhance immune function, promote escape behaviors, and suppress nonsurvival activities such as courtship or copulation (Sapolsky et al. 2000). However, at baseline levels, GCs promote energetic balance, by influencing processes such as foraging, and glucose and lipid mobilization, which allows individuals to meet daily energy requirements and the prolonged energetic expenditures associated with predictable life-history events (e.g., migration, rearing offspring) (Landys et al. 2006). Nevertheless, prolonged elevation over days to weeks (i.e., chronic stress) can negatively affect health and fitness (Sapolsky et al. 2000).

Unfortunately, given the general perception of GCs as only stress hormones, much of their application in conservation has been based on the generalized assumption that increases in GCs are always indicative of challenging or stressful environments (Bonier et al. 2009*a*; Busch & Hayward 2009). Viewed in this way, the interpretation of changing GC levels is appealing and easily applied. However, mounting evidence suggests GC physiology is much more complex (Romero 2005; Bonier et al. 2009*a*; Romero et al. 2009), making this approach controversial. Here we appeal to conservation biologists to take a predictive, physiological approach to the application of GCs to conservation goals in their study systems. We focus on 3 specific considerations that will improve conservation-based interpretation of GC levels across vertebrate taxa: a focus on baseline GC measures and their role in energetic balance; an understanding of the context-dependent nature of GC levels and their relationship to fitness; and a consideration of intra-individual variation in GC levels.

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Baseline Glucocorticoids as Integrators of Environmental Variability

Although measurement of the GC (stress) response has the potential to provide valuable insight into how organisms respond to acute environmental change (Romero 2005), we propose that either baseline levels (from plasma, serum, saliva) or integrated measures (from feces) are more practical and biologically relevant biomarkers for conservation biologists for 2 reasons. First, baseline levels can be obtained from a single sample, whereas stress-induced levels require 2 or more blood samples separated by a restraint protocol (Sheriff et al. 2011). Stress-induced methodology is often too invasive, impractical, or interferes with the goals of targeted recovery programs, especially in sensitive or protected species. Second, baseline GCs integrate many intrinsic and extrinsic environmental factors (Love et al. 2013) due to their primary role in energy regulation. As the difference between an individual's energetic requirements and the energy available (i.e., allostatic load) becomes larger, baseline GCs generally rise (McEwen & Wingfield 2003). Both environmental and social perturbations (e.g., changes in food abundance, predator pressure, social dominance, parasite load) can increase allostatic load because they raise the costs of maintaining energetic balance (McEwen & Windfield 2003). Given that many conservation-relevant disturbances can influence general energy expenditures or the ability of organisms to acquire sufficient resources, baseline GCs can provide a powerful reflection of organismal state. In addition, this perspective more easily allows for the essential interpretation of GC levels within the contexts of daily or seasonal changes (see below).

Prediction and Interpretation of Context-Dependent Glucocorticoid Levels

The application of GCs as effective biomarkers requires that GC levels can be interpreted as population-level indicators of environmental change or disturbance and that GCs show a predictable relationship with fitness, thereby indicating how populations will change demographically in response to environmental alterations (Bonier et al. 2009*a*; Busch & Hayward 2009; Cooke & O'Connor 2010). Higher GC levels have traditionally been assumed to be associated with an individual or population that is disturbed or in poorer condition and therefore of reduced relative fitness (Bonier et al. 2009*a*). This posited negative relationship between GCs and fitness is called the Cort fitness hypothesis and is principally based on the reasoning that high levels of GCs are indicative of individuals experiencing challenging conditions requiring reallocation of resources away from reproduction, thereby reducing fitness (Bonier et al. 2009*a*). However, a growing body of work in free-living systems indicates the relationship between GC physiology and the fitness-related traits that mediate population demography is not as simplistic (Romero 2005; Bonier et al. 2009*b*; Busch & Hayward 2009; Romero et al. 2009). Specifically, GC levels and their resultant relationship with fitness can vary based on a number of contexts including sex, age, life-history stage, and environmental quality (Bonier et al. 2009*b*; Angelier et al. 2010; Bonier et al. 2011). However, by placing emphasis on the primary energetic role of baseline GCs, conservation biologists can account for the context-dependent nature of GC levels and make informed predictions of how individuals will respond to an altered environment (Fig. 1). For example, elevated GCs during energetically expensive life-history stages such as breeding and migration do not necessitate that an organism is disturbed by its environment; instead, it can represent an adaptive response to promote beneficial foraging behavior, a phenomenon recently described by the Cort adaptation hypothesis (Romero 2002; Bonier et al. 2011). During stages of high reproductive investment (e.g., offspring provisioning), a positive relationship between baseline GCs and both reproductive success and survival has been observed (Bonier et al. 2009*a*, 2009*b*; Ouyang et al. 2011*a*). In this light, a decrease in baseline GCs during a normally energetically demanding stage could actually signal a disturbance.

Overall, this type of approach simultaneously considers the current state, investment level, and environmental conditions of the organism within a biologically relevant energetic framework. In addition, by combining baseline GC measures with other metrics of individual state (e.g., size-corrected body mass, fat stores, species-specific condition indices, reproductive investment metrics such as propagule number or number of dependent offspring), we can provide supplemental information to improve interpretations. Overall, by considering the fundamental energetic role of GCs, we move past simplified assumptions of GC physiology and formulate predictions of how GCs should change in the presence of a disturbance and what this will mean for a population of interest. On a broader scale, a consideration of the factors that can affect GCs and their relationship with fitness will also allow for the identification of patterns and improve their targeted application as a conservation biomarker across taxa.

Importance of Considering Intra-Individual Variability

It is assumed that the measurement of GCs from a sample of individuals over time is a reliable population-level

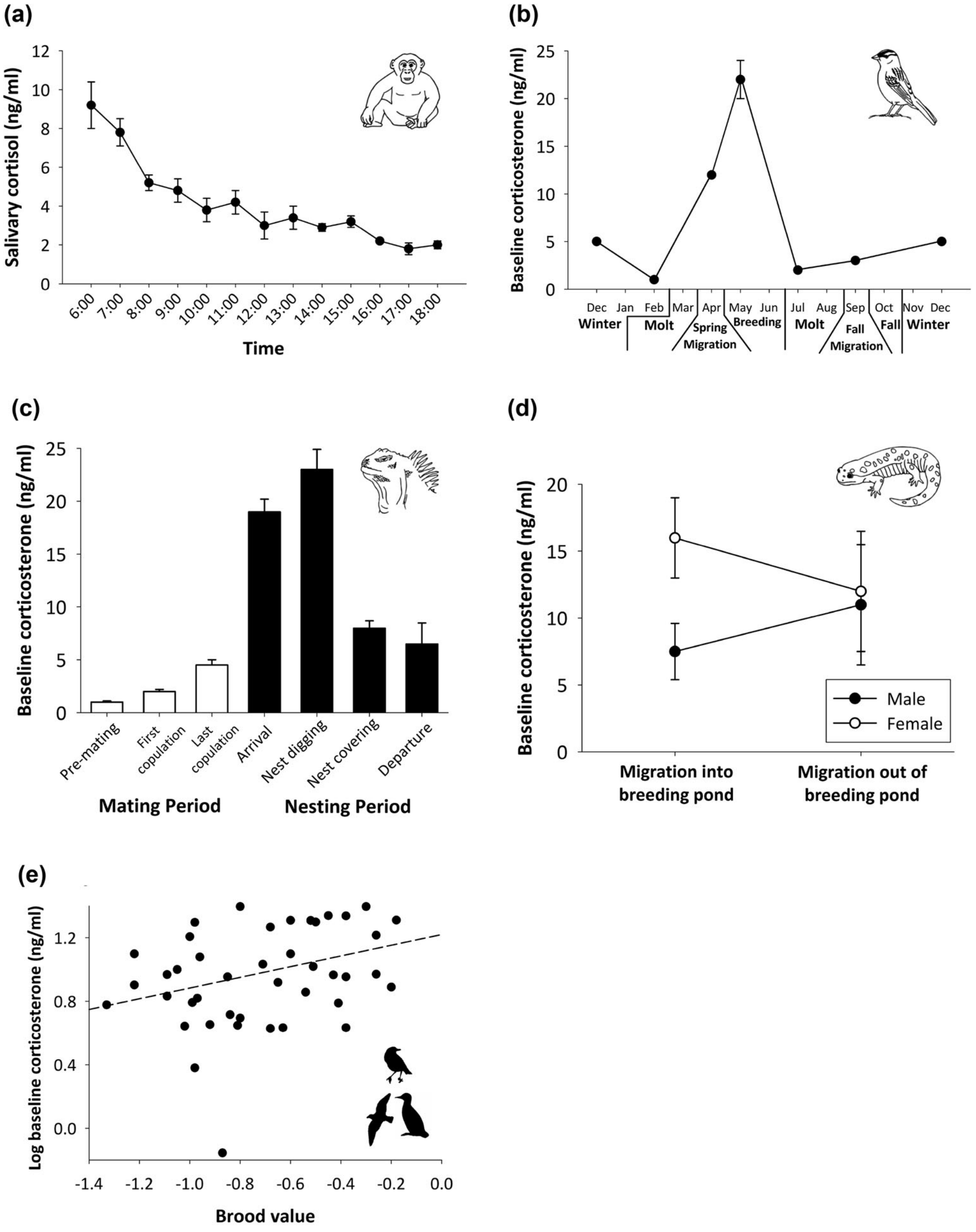

Figure 1. Contexts that cause variation in baseline glucocorticoid levels: (a) diel cycle (e.g., chimpanzee [P. troglodytes] [Heintz et al. 2011]); (b) season (e.g., White-crowned Sparrow ([Z. leucophrys gambelii] [Romero & Wingfield 1999]); (c) life stage within season (Galapagos marine iguana [A. cristatus] [Rubenstein & Wikelski 2005]); (d) sex (e.g., spotted salamander [A. maculatum] [Homan et al. 2003]); and (e) life history (e.g., phylogenetic comparative analysis of 64 avian species [Bokony et al. 2009] [brood value, value of the current reproductive attempt relative to lifetime reproductive output for a given species]). Figures redrawn from graphs in original publications. Graphs redrawn with permission from Heintz et al. 2011 (John Wiley and Sons), Romero & Wingfield 1999 (Elsevier), Rubenstein & Wikelski 2005 (Elsevier), Homan et al. 2003 (Elsevier), and Bokony et al. 2009 (University of Chicago Press).

indicator of disturbance, condition, and fitness (i.e., that monitoring the mean baseline GC values of subsamples of individuals over time represents a proxy of the overall population trend). However, to validate this assumption, we must determine whether baseline GCs fulfill 3 characteristics related to intra-individual variability. First, levels must be consistent within individuals under stable energetic or environmental conditions (Cooke & O'Connor 2010). The limited studies available on the repeatability of baseline GCs in wild populations have shown highly

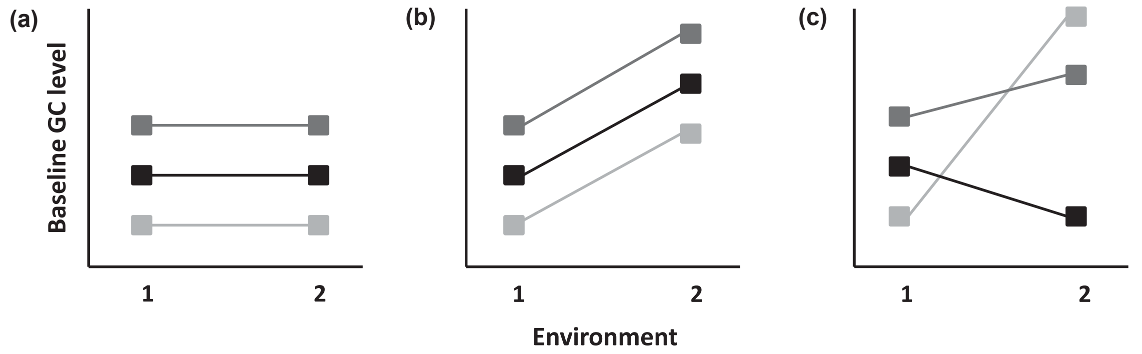

Figure 2. Scenarios depicting how baseline glucocorticoid (GC) levels of 3 individuals (light gray, black, and dark gray) can respond to a change in environmental quality (environment 1 and 2 on x-axis): (a, b) intra-individual changes in GC levels that can potentially be interpreted as population-level indicators of disturbance or condition, with the environmental change being benign or significant, respectively (a decrease in GC levels in [b] would be equally as interpretable) and (c) individuals respond differently, or in individually specific ways, to the same change in the environment, constraining the ability to interpret the physiological change as an indication of population state.

variable results (Ouyang et al. 2011*b*), and future studies that specifically control for changes in underlying environmental conditions between measurements are therefore required. Second, individual GC levels must change in a similar (i.e., predictable) way in response to an environmental change (Fig. 2). Targeted investigations of this characteristic are lacking and will require an experimental approach that manipulates specific environmental conditions. Finally, levels must show a consistent relationship with fitness metrics within individuals (Dingemanse et al. 2010). Indeed, Bonier et al. (2009*b*) observed a change in the GC-fitness relationship within individuals, from negative during early breeding to positive during late breeding, indicating the importance of investigating this characteristic. Overall, there has been limited focus on these important aspects of the conservation-based application of GCs. However, this type of validation is necessary to draw inferences on population disturbance by comparing GC levels among individuals in different habitats and for the monitoring of GC levels over time to be informative. We urge conservation biologists to be aware of the assumptions related to intra-individual variability when interpreting GC levels and contribute to the investigation of the characteristics within their study systems where possible.

Final Considerations

Although the application of GC measures to conservation biology is still developing, a predictive approach rooted in the context-dependent, physiological role of GCs can alleviate many of the pitfalls related to the perception of GCs as simply stress hormones. In addition, researchers should avoid classifying activities as stressors prior to investigating their effects. Monitoring individuals across a gradient of environmental change will help determine whether, and at what intensity, an activity begins to alter physiology. Because most research has been conducted in avian systems, investigations in other taxa will help determine which broad contexts are most important, and supplemental information within species will help refine whether a specific sex, age class, or life-history stage is best suited for a GC-based technique. Conservation biologists will benefit if they consider these and other contexts specific to their system (e.g., dominance hierarchy or migratory expenditures) when choosing sampling times and interpreting GC levels. Luckily, species-specific studies that consider the real-world applicability of results are mounting, improving the ability of conservation managers to determine whether GC physiology will be a valuable tool in their study system. A strong interdisciplinary approach that emphasizes the energetic role of GCs, incorporates the context-dependency of such levels, and considers intra-individual variability will greatly enhance the relevance of GC physiology for conservation management.

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