ORNITOLOGIA NEOTROPICAL 19 (Suppl.): 207–218, 2008

# STRESS HORMONES IN TROPICAL BIRDS: PATTERNS AND FUTURE DIRECTIONS

**Lynn B. Martin II[1] & Dustin R. Rubenstein[2]**

[1]Division of Integrative Biology, Department of Biology, University of South Florida, Tampa Florida 33620, USA. *E-mail:* lmartin@cas.usf.edu

[2]Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley California 94720, USA

**Resumen. – Las hormonas del estrés en aves tropicales: patrones y direcciones para el futuro. –** Las glucocorticoides son unas hormonas estresantes importantes que afectan muchos aspectos fisiológicos y de conducta en las aves. Aunque estas hormonas se han estudiado muy bien en aves de regiones templadas y de aves moradoras (dwelling) del Ártico, es muy poco lo que se sabe en las especies tropicales. La corticosterona, la glucocorticoide aviaria primaria, es mejor conocida por su participación en el balance de la energía. En contextos ecológicos, su función principal es el re-dirigir el organismo hacia la sobrevivencia inmediata de un estresor biótico o abiótico. Como los medio ambientes tropicales son diferentes de los de regiones templadas y Árticas, la corticosterona puede tener una influencia exclusiva en la fisiología aviaria y en la conducta de las aves cerca del ecuador. Por ejemplo, las estaciones en el trópico no se caracterizan por los cambios dramáticos en la temperatura del ambiente como ocurre en las zonas templadas y el Ártico. En el trópico, otras circunstancias, como la precipitación pluvial, pueden tener una influencia más fuerte en la corticosterona y, por lo tanto, en el buen estado de salud del ave. De la misma manera, la amenaza de infecciones puede ser mayor, o por la menos, más persistente en las áreas tropicales comparadas con otras partes del mundo. Como la corticosterona puede ser inmunosupresiva, las aves tropicales pueden evitar mantener un número alto de los niveles de esta hormona o pueden ser indeferentes a esta. En este trabajo, se revisan los aspectos básicos de la fisiología de la glucorticoide y, luego, se resumen brevemente los trabajos existentes de la corticosterona en aves no tropicales. Luego, se resumen los datos de los pocos estudios de la corticosterona en especies tropicales y se sugiere una guía potencialmente útil para futuros estudios, incluyendo como las diferencias del hábitat y las relaciones sociales y de apareamiento en particular pueden influenciar los patrones de la corticosterona en las especies tropicales. Como la corticosterona puede ser un indicador del estrés que ha experimentado un organismo, el estudio de esta hormona en aves tropicales puede enseñarnos, no sólo como funciona en situaciones nuevas, sino también aumentar los esfuerzos para conservar la población aviaria.

**Abstract. –** Glucocorticoids are important stress hormones in birds that affect many aspects of physiology and behavior. Although these hormones have been well studied in temperate and Arctic-dwelling birds, much less is known about them in tropical species. Corticosterone, the primary avian glucocorticoid, is best-known for its involvement in energy balance. In ecological contexts, its main function is to re-direct an organism towards immediate survival of a biotic or abiotic stressor. As tropical environments are quite different from temperate and Arctic ones, corticosterone may have unique influences on avian physiology and behavior near the equator. For example, seasonality in the tropics is not characterized by the dramatic changes in ambient temperature as it is in the Arctic and temperate zones. In the tropics, other conditions, such as rainfall, may more strongly influence corticosterone and thus fitness. Likewise, threat of infection may be greater, or at least more persistent, in the tropics compared to other parts of the globe. As corticosterone can be immunosuppressive, tropical birds may avoid maintaining high levels of this hormone or be insensitive to it. In this paper, we review basic aspects of glucocorticoid physiology then briefly summarize the literature on corticosterone in non-tropical birds. We then summarize data from the few studies of corticosterone in tropical species and suggest some potentially useful directions for future studies, including how differences in habitat and social/mating systems, in particular, might influence patterns of corticosterone in tropical species. As corticosterone can be an indicator of the stress an organism has experienced, study of this hormone in tropical birds may not only teach us about its function in novel situations, it may also augment efforts to conserve avian populations. *Accepted 19 October 2007.*

**Key words:** Corticosterone, immune, life history, physiology, stress hormones.

## INTRODUCTION

Glucocorticoids (GCs) are steroid hormones that regulate many aspects of vertebrate physiology and behavior (Sapolsky *et al.* 2000). The primary GC in birds is corticosterone (Wingfield & Hunt 2002), which circulates at low levels (hereafter baseline) in the blood and predominantly regulates energy balance (Sapolsky *et al.* 2000). Corticosterone (CORT) baselines fluctuate daily in birds, typically reaching a maximum at the onset of the active period (Romero & Remage-Healey 2000; Tarlow *et al.* 2003), and also seasonally, reaching a low during molt and a peak during breeding (Romero 2002). CORT is often referred to as a "stress hormone" because levels in the blood rise in response to a variety of abiotic (e.g., inclement weather) and biotic (e.g., changes in social rank, aggressive interactions, predation) stressors (McEwen & Wingfield 2003). These CORT elevations (hereafter stress-induced levels) regulate a variety of physiological processes that collectively increase short-term survival probability (Sapolsky *et al.* 2000).

An effective way to characterize the functional significance of CORT is through the emergency life-history concept (Wingfield *et al.* 1998). Birds and most other organisms progress through a series of life stages (e.g., breeding, molting, over-wintering, and migration) that are triggered by changes in environmental conditions (Jacobs & Wingfield 2000). In response to stressors such as a predation event, a food shortage, or an antagonistic encounter with a conspecific (McEwen & Wingfield 2003), CORT surges in circulation and moves the organism out of the prevailing life stage and into an emergency state. In this emergency state, energy and resources are shunted away from physiological processes promoting the original state and towards functions promoting survival (Wingfield *et al.* 1998). Some CORT-induced changes during emergencies include increased cardiovascular tone, heightened immune surveillance, enhanced memory consolidation, and decreased libido (Sapolsky *et al.* 2000). CORT stress responses are thus adaptive strategies that allow individuals to cope with unpredictable environmental perturbations (McEwen & Wingfield 2003).

To date, CORT has been well-studied in birds from temperate and Arctic zones, but comparatively little is known about this hormone in birds living at latitudes below 20 degrees. After providing a basic overview of CORT physiology in vertebrates, we briefly review the literature on CORT in non-tropical birds. We then compare and contrast these studies with the few data available for tropical species and discuss possible future directions for studying CORT in tropical birds.

## CORTICOSTERONE PHYSIOLOGY

CORT secretion is predominantly regulated

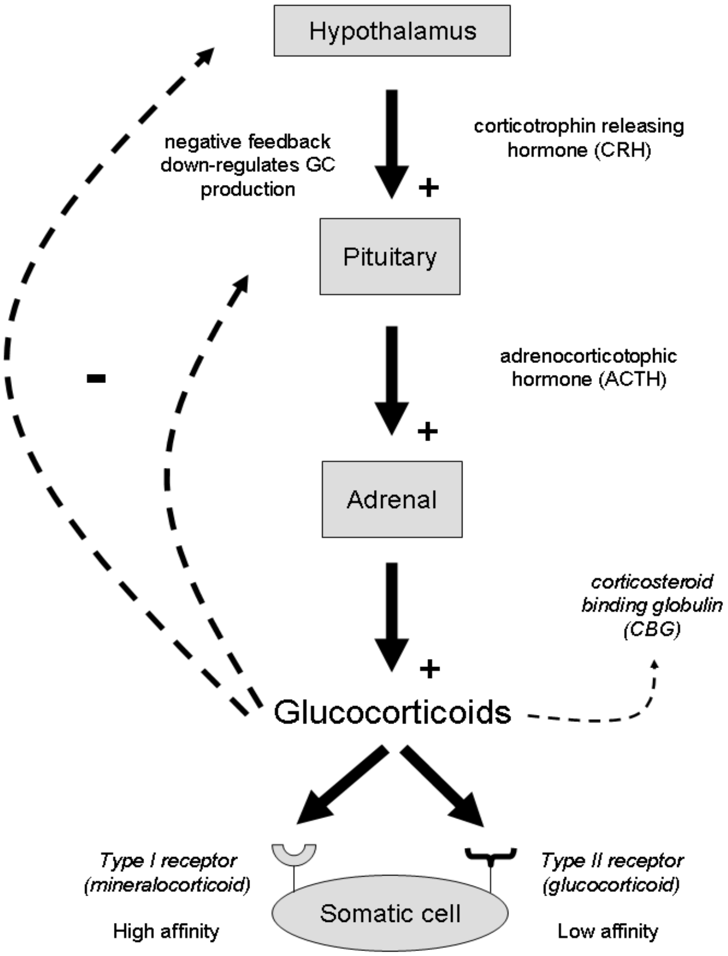

FIG. 1. The vertebrate hypothalamo-pituitary-adrenal axis. Shaded boxes depict the two brain areas producing protein hormones to drive glucocorticoid (GC) production; the third box represents the adrenal gland, which is responsible for most GC synthesis in birds. Solid descending arrows between boxes depict direction of hormonal cascade from brain to adrenal glands; plusses (+) demarcate stimulatory effects of protein hormones (corticotrophin-releasing hormone and adrenocorticotrophic hormone) on GC production. Shaded ovoid represents a generic somatic cell and the two types of GC receptors (I and II) cells can possess. Horizontal dashed line depicts potential interaction between GCs and binding globulins in circulation (see text for detail). Ascending dashed lines indicate negative effects of elevated GCs on subsequent GC production (i.e., negative feedback).

by the hypothalamo-pituitary-adrenal (HPA) axis (Fig. 1). The peptide hormone, corticotrophin releasing hormone (CRH), is secreted by the hypothalamus and stimulates the release of adrenocorticotropic hormone (ACTH) from the anterior pituitary, which in turn stimulates CORT secretion by the adrenal glands. CORT levels are ultimately regulated via negative feedback; once CORT reaches a certain threshold in circulation, receptors in the brain down-regulate CRH and ACTH release causing CORT secretion to slow. There are two types of CORT receptors found in most cell types in the body (Sapolsky *et al.* 2000). Type 1 (mineralocorticoid) receptors have high affinity for CORT and tend to be activated when circulating CORT is low (i.e., baseline levels). Type 2 (glucocorticoid) receptors, however, have low affinity for CORT and are predominantly activated only in response to stressors (Romero 2004). Type 1 receptors often have permissive effects that facilitate other components of the stress response, whereas Type 2 receptors are actively stimulatory or inhibitory depending on context (Romero 2004). Another important component of the HPA axis is the corticosteroid binding globulins, or CBG's (Breuner *et al.* 2003). Although it is unclear whether binding globulins chaperone CORT within the circulation and thus promote CORT actions, or whether they effectively buffer CORT from interacting with receptors (Romero 2004), they likely play an important but underappreciated role in avian stress physiology.

## CORTICOSTERONE IN ARCTIC AND TEMPERATE BIRDS

CORT is well-studied in birds living in Arctic (Wingfield & Hunt 2002) and temperate areas (Breuner *et al.* 2003; Romero 2002). One of the best-studied species is the White-crowned Sparrow (*Zonotrichia leucophrys*) (Wingfield *et al.* 2008). HPA activity in high-latitude *Zonotrichia* subspecies is representative of other Arctic passerines; in *Zonotrichia* (i) stress-induced CORT levels vary seasonally, becoming damped during the period when offspring are being provisioned, (ii) CORT secretion is controlled at multiple points along the HPA axis, and (iii) experimental elevation of baseline CORT levels has weak effects on behavior, especially during breeding (Wingfield & Hunt 2002). Collectively, the failure of Arctic birds to respond to elevated CORT during breeding is thought to ensure successful reproduction and complete molt prior to migration in the short window of time available for breeding in the Arctic (Breuner *et al.* 2003). Studies of mid-latitude birds have indirectly supported this theory; in the United States (Wada *et al.* 2004; Wilson & Holberton 2004) and Europe (Goymann *et al.* 2006; Silverin & Wingfield 1998), experimental elevations in CORT dramatically reduced parental behavior in a variety of avian species.

## CORTICOSTERONE IN TROPICAL BIRDS

Most studies of CORT in tropical birds have also focused on how it influences behavior. One example of how CORT may influence behavior in tropical species comes from studies of siblicide in boobies. Nazca Boobies (*Sula granti*) are long-lived seabirds that typically lay two eggs, but because of hatching asynchrony, the first-laid offspring is always much larger than the second. The second-laid offspring rarely reaches adulthood because the first-laid offspring out-competes, or even kills it (Anderson 1989). Baseline CORT was higher in first-laid offspring from two-egg nests compared to chicks from single egg nests (Tarlow *et al.* 2001), suggesting that CORT may induce (or facilitate) siblicidal behavior. Similar patterns were detected in the Blue-footed Booby (*Sula nebouxii*), where CORT levels were 109% lower in second-laid offspring compared to first-laid offspring or singletons (de la Mora *et al.* 1996). Artificial elevation of CORT in subordinates (via implant) did not increase begging behavior, but it did affect parental provisioning rate because of increased activity in first-laid offspring (Vallarino *et al.* 2006). In this system, CORT may influence aggression when siblings are of similar size: experimental pairing of singletons with dominants and singletons with subordinates led to CORT elevations in singletons and dominants, but not subordinates (Ramos-Fernandez *et al.* 2000). Environmental conditions at the time of nesting can also influence chronic levels of baseline CORT in this species, and thus impact reproduction. In 1992, reproduction in one Blue-footed Booby colony failed completely, presumably because of a large El Niño event that year, and CORT titers were higher in females during the parental care stage compared to the same stage a year later (Wingfield *et al.* 1999).

The effects of CORT on behavior are not limited to seabirds. European populations of Stonechats (*Saxicola torquata rubicola*) often begin second clutches before nestlings fledge. African populations (*S. t. axillaris*), however, endure a long post-fledging care period before initiating subsequent clutches (Konig & Gwinner 1995). The breeding strategy of African populations may be related to higher nest predation in the tropics (Ghalambor & Martin 2001). African Stonechats rearing offspring in territories in which a predator [the Fiscal Shrike (*Lanius collaris*)] was present delayed successive broods (Scheuerlein *et al.* 2001). CORT appeared to influence these delays in reproduction, at least in part; adult males had higher CORT in territories with shrikes than in territories without.

CORT also influences the adoption of different breeding roles in some tropical species. The relationship between CORT and helping behavior in birds has been investigated in temperate species, but neither baseline nor stress-induced CORT predicted breeding roles in Florida Scrub Jays (*Aphelocoma coerulescens*) (Schoech *et al.* 1991; Schoech *et al.* 1997), and baseline levels did not predict breeding roles in Harris Hawks [*Parabuteo unicinctus* (Mays *et al.* 1991)]. In one species of tropical passerine (Zambian White-browed Sparrow Weavers (*Plocepasser mahali*), baseline CORT was not related to breeding role (Wingfield *et al.* 1991; Wingfield *et al.* 1992). However, in Superb Starlings (*Lamprotornis superbus*) from Kenya, CORT was related to the adoption of different breeding roles (Rubenstein 2007); both baseline and stress-induced CORT levels, which were related to the amount of rainfall prior to breeding, predicted breeding role, but only in subordinate helpers, not in dominant breeders.

Two final examples of work on CORT in tropical birds come from *Zonotrichia* and *Passer* sparrows. As noted above, Arctic and temperate White-crowned Sparrows exhibited seasonal variation in both CORT levels and CBG-binding capacity (Breuner *et al.* 2003; Wingfield & Hunt 2002). Near-equatorial Rufous-collared Sparrows (*Zonotrichia capensis*) also exhibited seasonality in CORT levels with higher values of CORT occurring during breeding versus molting (Wada *et al.* 2006). Unlike temperate and Arctic species, however, neither CORT nor CBG capacity varied between males and females in tropical *Zonotrichia.* More study is needed, but these differences may be related to the unique environments and/or life histories of species living in these different areas.

In the case of the House Sparrows (*Passer domesticus*), variation in CORT appears related to the threat of infection. Threat of infection was found to be more persistent (Martin *et al.* 2007) and investments in immune defense investments greater (Martin *et al.* 2006; Martin *et al.* 2004) in a tropical Panamanian population of House Sparrows than in a North American (New Jersey) population. Additionally, Panamanian House Sparrows had lower baseline CORT and exhibited weaker CORT stress responses than North American sparrows (Martin *et al.* 2005). The authors speculated that low CORT might promote the higher immune investments in the tropical population. This hypothesis was tested by experimentally elevating CORT (via implant) in both populations because long-term elevation of CORT in temperate animals suppresses immune activity (Sapolsky *et al.* 2000). As predicted, immune activity was suppressed by CORT in temperate birds, but not tropical birds (Martin *et al.* 2005). It is premature to state that all tropical species are immunologically insensitive to CORT, however. House Sparrows are an invasive species, so immunological insensitivity to CORT may be related to their recent arrival to the Neotropics. Further, handling stress, which elevates CORT in birds (Romero & Romero 2002), suppressed immune activity in several tropical species (Matson *et al.* 2006). Further work on the influence of CORT on immune activity in tropical birds is thus important.

## LATITUDINAL PATTERNS IN CORTICOSTERONE

As in temperate birds, CORT influences a broad range of behaviors and physiological processes in tropical species. It remains unclear, however, to what extent latitudinal variation in CORT explains differences in behavior and life history between tropical and temperate/Arctic species. Birds show latitudinal variation in many traits including clutch size (Lack 1947; Martin 1996), length of the incubation period (Martin 2002; Ricklefs 1992), adult survival probability (Karr *et al.* 1990), investment in immunity (Martin *et al.* 2006), and rates of energy turnover (Wikelski *et al.* 2003b). Although multiple studies in the temperate zone have also detected latitudinal variation in CORT (Breuner *et al.* 2003; Silverin & Wingfield 1998; Wada *et al.* 2006; Wilson & Holberton 2004), few studies have included tropical populations in these comparisons. Thus, it remains unknown whether tropical birds exhibit comparatively stronger CORT responses to stressors as predicted by previous studies (Breuner *et al.* 2003). The limited data show mixed evidence of latitudinal patterns. Tropical House Sparrows exhibited weaker, not stronger, CORT responses to a stressor than North America individuals (Martin *et al.* 2005). In contrast, CORT responses in Ecuadorian Rufous-collared Sparrows (Wada *et al.* 2006), Kenyan Superb Starlings (Rubenstein 2007), and Kenyan Stonechats (Goymann *et al.* 2006) were generally similar to temperate and/or Arctic congeners or confamiliars. Baseline CORT levels were higher in North American European Starlings than in African Superb Starlings, but the magnitudes of the stress responses were similarly high (Romero & Remage-Healey 2000; Rubenstein 2007). Moreover, the direction of variation was reversed in Stonechats, with African birds maintaining higher baseline levels than European ones (Goymann *et al.* 2006). Perhaps there is as much variation within the tropics as across latitudes; only additional data can refute this possibility.

## FUTURE DIRECTIONS

The above examples highlight the value of studying CORT in tropical birds. However, they also reveal the current shortage of data in near-equatorial species. Gaining a better understanding of how CORT affects behavior and physiology in tropical species requires an appreciation of how both biotic and abiotic factors influence CORT. A variety of different environmental and social factors affect CORT in non-tropical species (McEwen & Wingfield 2003). It will be important to determine if these and other factors influence avian stress physiology in tropical species, and if they do so in the same manner. It is known that testosterone, another steroid hormone, is influenced by both environmental conditions

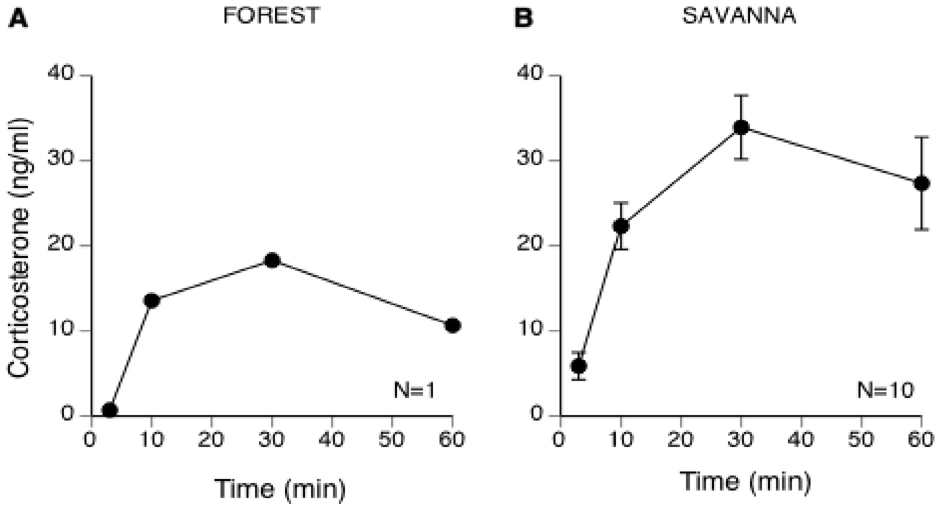

FIG. 2. Glucocorticoid stress responses in Common Bulbuls (*Pycnonotus barbatus*) from (A) forest (Kakamega Forest, 0°13'28N, 34°54'E) and (B) savanna (Mpala Research Centre, 0°17'N, 37°52'E) in Kenya. Samples were collected < 3, 10, 30 and 60 min after capture. Mean ± SE are shown. Samples sizes are indicated under each curve. Both sites are at roughly the same altitude (~1650 m) and samples were collected post-breeding (August 2004).

and inter-specific differences in social and mating systems in tropical species (Wikelski *et al.* 2003a; Wikelski *et al.* 1999). Also, latitudinal variation in testosterone has been predicted to mediate some of the latitudinal patterns in life history characters in birds (Goymann *et al.* 2004; Hau 2007). We expect that CORT will likewise be revealed as a mediator of life history variation in birds and begin exploring this possibility here.

*Environmental conditions.* Strong CORT stress responses in the tropics were initially predicted based upon the assumption that tropics are benign, relatively stable environments that allow for long breeding seasons (Martin 1996, Hau 2007). As large portions of the tropics are not temporally predictable (Rubenstein & Lovette 2007), however, the length of the breeding season, and thus CORT levels, are likely to be greatly influenced by small-scale variation in habitat and related environmental factors. For example, tropical savannas are unpredictable environments, characterized by high temporal variability in rainfall (Rubenstein & Lovette 2007), which influences baseline and stress-induced CORT levels, reproductive behavior, and life history traits in birds (Perfito *et al.* 2007; Rubenstein 2007). Desert islands are similarly climatically erratic and, in these areas (e.g., the Galapagos archipelago), birds adjust their reproductive behavior to account for this environmental unpredictability (Hau *et al.* 2004). Even moist, lowland tropical forests exhibit dramatic intra-annual fluctuations in rainfall (Wikelski *et al.* 2003a). Preliminary support for intra-tropical variation in CORT comes from comparisons in Common Bulbuls (*Pycnonotus barbatus*). Despite small sample sizes that preclude statistical analyses, stress-induced, but not baseline, CORT was lower in bulbuls from forested than savannah habitats (Fig. 2). No individuals were molting and all were in

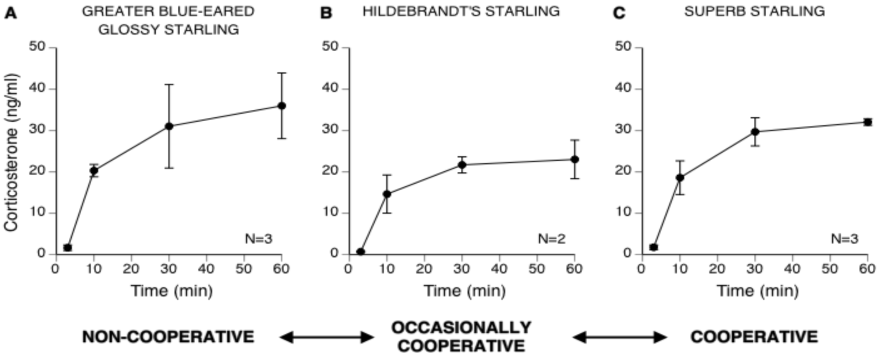

FIG. 3. Glucocorticoid stress responses in co-occurring *Lamprotornis* starlings with different social systems. The (A) Greater Blue-eared Glossy Starling (*L. chalybaeus*) is a non-cooperative breeder, the (B) Hildebrandt's Starling (*L. hildebrandti*) is an occasional cooperative breeder, and (C) the Superb Starling (*L. superbus*) is an obligate cooperative breeder. Samples were collected < 3, 10, 30 and 60 min after capture. Mean ± SE are shown. Samples sizes are indicated below each curve. All samples were collected in July 2005 (over a 14-day period during the dry season) at the Mpala Research Centre, Kenya, after all species had completed breeding.

roughly the same life history stage (i.e., post-breeding), indicating that variation could be due to habitat of residence.

Although differences in predictability of precipitation and food availability in different tropical habitats could directly influence CORT levels in tropical birds, there are several other possible explanations to explain inter-habitat CORT differences. For instance, individuals may be more densely packed in some habitats than others, which would lead to increased competition for resources [i.e., Ashmole's hypothesis, *sensu* (Ricklefs 2000)] and perhaps elevated CORT (Nephew & Romero 2003). Strong CORT responses in birds experiencing such conditions might help mobilize energy stores for sustained aggressive activity, or redistribute immune resources rapidly to peripheral sites where wounding might occur, both of which could improve survival probability. However, in habitats where stressors would be common, strong CORT responses could also be detrimental. For example, CORT responses can increase oxidative tissue damage (Sapolsky *et al.* 2000), which would compromise individual survival (Martin 1996). As many tropical forest birds exhibit low rates of mortality (Karr *et al.* 1990), strong CORT responses may be unfavorable, and thus particularly low in habitats where average survival rates are high (e.g., forests). Altitude may also affect CORT variability within the tropics. At high altitudes, CORT responses tend to be damped in temperate passerines (Pereyra & Wingfield 2003). Furthermore, important life history characters that influence CORT, such as duration of the breeding season (Perfito *et al.* 2004), can differ dramatically between populations separated by only short vertical distances.

*Social and mating systems.* Differences in social and mating systems influence interspecific variation in testosterone in birds (Goymann *et al.* 2007; Wingfield *et al.* 2001), and may drive interspecific CORT patterns as well. To date, this possibility has not been explored in birds, regardless of latitude. As a preliminary test of this hypothesis, baseline and stress-induced CORT were quantified in three species of sympatric *Lamprotornis* starlings with different social systems after the breeding season: (i) the non-cooperatively breeding Greater Blue-eared Glossy Starling (*Lamprotornis chalybaeus*), (ii) the occasionally cooperatively breeding Hildebrandt's Starling (*Lamprotornis hildebrandti*), and (iii) the obligate cooperatively breeding Superb Starling (Rubenstein unpubl.). In all three species, baseline CORT was very low (means $< 1.8$ ng ml$^{-1}$), but all species mounted robust CORT responses to stressors (Fig. 3) that were comparable in magnitude to temperate European Starlings (Romero & Remage-Healey 2000). Although no marked differences existed between baseline and stress response CORT among species, sample sizes for all species were small and sampling occurred during the non-breeding season. Based on extensive work in one of these species, baseline CORT appears to mediate selection of breeding role only prior to the breeding season (Rubenstein 2007). Further work with larger samples sizes and with greater temporal coverage in species with different mating systems is critical. Additionally, consideration of the influence of CORT on role procurement in different social and mating systems (e.g., lekking manakins) would be especially insightful from Neotropical birds given the plethora of life history and ecological data that exist for these species.

## CONCLUSIONS

Although the lack of data makes generalizations about CORT in tropical birds impossible at present, there is much to be gained from future studies, particularly in the Neotropics. Comparisons of circulating CORT alone, however, are unlikely to reveal the function of CORT in tropical birds; experimental manipulation of the HPA axis in a variety of contexts is critical. Indeed, to gain functional insight into CORT actions in tropical birds, the complexity of HPA activity must be taken into account. Arctic and temperate species regulate CORT at different points of the HPA axis (Wingfield & Hunt 2002), and the site of regulation often changes depending on the time of year (Breuner *et al.* 2003). Regulation of CORT production by the HPA axis is also not the only option available to birds; local regulation (e.g., at the tissue level) may also be possible. Some organs in domesticated fowl can produce all of the components of the HPA axis (Lechner *et al.* 2001). Perhaps some birds regulate CORT at the level of the tissue more so than the whole body. This strategy could be particularly beneficial for tropical birds because it would allow them to avoid the potentially damaging side-effects of chronically-elevated CORT.

Research on CORT in tropical birds would also have applied benefits. Ecotourism constitutes a large component of the income of many tropical economies. The consequences of ecotourism on the native fauna are rarely considered, but it is becoming clear that just the presence of tourists can affect CORT, and perhaps fitness (Walker *et al.* 2008). For example, juvenile Hoatzins (*Opisthocomus hoazin*) at Cuyabeno Reserve in Ecuador had elevated CORT responses to stressors and exhibited lower survival probability in areas frequented by tourists compared to reference sites (Mullner *et al.* 2004). The great diversity of species and behaviors in the Neotropics provides an outstanding opportunity for understanding CORT in both applied and basic contexts that do not occur at high latitudes.

## ACKNOWLEDGMENTS

We thank the conveners of the VIII NOC for the opportunity to contribute to this special issue, and John Wingfield for coordinating the symposium. We also acknowledge the other participants in the symposium for advice and constructive comments on earlier drafts. LBM thanks Martin Wikelski and Randy J. Nelson for support to participate in the congress. DRR acknowledges a fellowship from the Miller Institute for Basic Research at the University of California, Berkeley.

## REFERENCES

Anderson, D. J. 1989. The role of hatching asynchrony in siblicidal brood reduction of two booby species. Behav. Ecol. Sociobiol. 25: 363–368.

Breuner, C. W., M. Orchinik, T. P. Hahn, S. L. Meddle, I. T. Moore, N. T. Owen-Ashley, T. S. Sperry, & J. C. Wingfield. 2003. Differential mechanisms for regulation of the stress response across latitudinal gradients. Am. J. Physiol. Regul. Integr. Comp. Physiol. 285: R594–R600.

de la Mora, A. N., H. Drummond, & J. C. Wingfield. 1996. Hormonal correlates of dominance and starvation-induced aggression in chicks of the Blue-footed Booby. Ethology 102: 748–761.

Ghalambor, C. K., & T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292: 494–497.

Goymann, W., I. T. Moore, A. Scheuerlein, K. Hirschenhauser, A. Grafen, & J. C. Wingfield. 2004. Testosterone in tropical birds: Effects of environmental and social factors. Am. Nat. 164: 327–334.

Goymann, W., D. Geue, I. Schwabl, H. Flinks, D. Schmidl, H. Schwabl, & E. Gwinner. 2006. Testosterone and corticosterone during the breeding cycle of equatorial and European stonechats (*Saxicola torquata axillaris* and *S. t. rubicola*). Horm. Behav. 50: 779–785.

Goymann, W., M. M. Landys, & J. C. Wingfield. 2007. Distinguishing seasonal androgen responses from male-male androgen responsiveness – revisiting the challenge hypothesis. Horm. Behav. 51: 463–476.

Hau, M. 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. Bioessays 29: 133–144.

Hau, M., M. Wikelski, H. Gwinner, & E. Gwinner. 2004. Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. Oikos 106: 489–500.

Jacobs, J. D., & J. C. Wingfield. 2000. Endocrine control of life-cycle stages: A constraint on response to the environment? Condor 102: 35–51.

Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, & J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests – will the dogma survive. Am. Nat. 136: 277–291.

Konig, S., & E. Gwinner. 1995. Frequency and timing of successive broods in captive African and European stonechats *Saxicola torquata axillaris* and *Saxicola torquata rubicola*. J. Avian Biol. 26: 247–254.

Lack, D. 1947. The significance of clutch sizes. Ibis 89: 302–352.

Lechner, O., H. Dietrich, G. J. Wiegers, M. Vacchio, & G. Wick. 2001. Glucocorticoid production in the chicken bursa and thymus. Int. Immunol. 13: 769–776.

Martin, L. B., M. I. Pless, J. Svoboda, & M. Wikelski. 2004. Immune activity in temperate and tropical House Sparrows: A common-garden experiment. Ecology 85: 2323–2331.

Martin, L. B., J. Gilliam, P. Han, K. A. Lee, & M. Wikelski. 2005. Corticosterone suppresses cutaneous immune function in temperate but not tropical House Sparrows, *Passer domesticus*. Gen. Comp. Endocrinol. 140: 126–135.

Martin, L. B., D. Hasselquist, & M. Wikelski. 2006. Immune investments are linked to pace of life in House Sparrows. Oecologia 147: 565–575.

Martin, L. B., M. I. Pless, & M. Wikelski. 2007. Greater seasonal variation in blood and ectoparasite infections in a temperate than a tropical population of House Sparrows (*Passer domesticus*) in North America. Ibis 149: 419–423.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? J. Avian Biol. 27: 263–272.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proc. Roy. Soc. Lond. B Biol. Sci. 269: 309–316.

Matson, K. D., B. I. Tieleman, & K. C. Klasing. 2006. Capture stress and the bactericidal competence of blood and plasma in five species of tropical birds. Physiol. Biochem. Zool. 79: 556–564.

Mays, N. A., C. M. Vleck, & J. Dawson. 1991. Plasma luteinizing-hormone, steroid-hormones, behavioral role, and nest stage in cooperatively breeding Harris Hawks (*Parabuteo unicinctus*). Auk 108: 619–637.

McEwen, B. S., & J. C. Wingfield. 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43: 2–15.

Mullner, A., K. E. Linsenmair, & M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in Hoatzin chicks (*Opisthocomus hoazin*). Biol. Conserv. 118: 549–558.

Nephew, B. C., & L. M. Romero. 2003. Behavioral, physiological, and endocrine responses of starlings to acute increases in density. Horm. Behav. 44: 222–232.

Pereyra, M. E., & J. C. Wingfield. 2003. Changes in plasma corticosterone and adrenocortical response to stress during the breeding cycle in high altitude flycatchers. Gen. Comp. Endocrinol. 130: 222–231.

Perfito, N., A. D. Tramontin, S. Meddle, P. Sharp, D. Afik, J. Gee, S. Ishii, M .Kikuchi, & J. C. Wingfield. 2004. Reproductive development according to elevation in a seasonally breeding male songbird. Oecologia 140: 201–210.

Perfito, N., R. A. Zann, G. E. Bentley, & M. Hau. 2007. Opportunism at work: habitat predictability affects reproductive readiness in free-living Zebra Finches. Func. Ecol. 21: 291–301.

Ramos-Fernandez, G., A. Nunez-de la Mora, J. C. Wingfield, & H. Drummond. 2000. Endocrine correlates of dominance in chicks of the Blue-footed Booby (*Sula nebouxii*): testing the Challenge hypothesis. Ethol. Ecol. Evol. 12: 27–34.

Ricklefs, R. E. 1992. Embryonic development period and the prevalence of avian blood parasites. Proc. Natl. Acad. Sci. USA 89: 4722–5.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102: 9–22.

Romero, L. M. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen. Comp. Endocrinol. 128: 1–24.

Romero, L. M. 2004. Physiological stress in ecology: lessons from biomedical research. Trends Ecol. Evol. 19: 249–255.

Romero, L. M., & L. Remage-Healey. 2000. Daily and seasonal variation in response to stress in captive starlings (*Sturnus vulgaris*): Corticosterone. Gen. Comp. Endocrinol. 119: 52–59.

Romero, L. M., & R. C. Romero. 2002. Corticosterone responses in wild birds: The importance of rapid initial sampling. Condor 104: 129–135.

Rubenstein, D. R. 2007. Stress hormones and sociality: integrating social and environmental stressors. Proc. Roy. Soc. Lond. B Biol. Sci. 274: 967–975.

Rubenstein, D. R., & I. J. Lovette. 2007. Environmental unpredictability drives the evolution of cooperative breeding in birds. Curr. Biol. 17: 1414–1419.

Sapolsky, R. M., L. M. Romero, & A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 21: 55–89.

Scheuerlein, A., T. J. Van't Hof, & E. Gwinner. 2001. Predators as stressors? Physiological and reproductive consequences of predation risk in tropical Stonechats (*Saxicola torquata axillaris*). Proc. Roy. Soc. Lond. B Biol. Sci. 268: 1575–1582.

Schoech, S. J., R. L. Mumme, & M. C. Moore. 1991. Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida Scrub Jays (*Aphelocoma coerulescens*). Condor 93: 354–364.

Schoech, S. J., R. L. Mumme, & J. C. Wingfield. 1997. Corticosterone, reproductive status, and body mass in a cooperative breeder, the Florida Scrub-Jay (*Aphelocoma coerulescens*). Physiol. Zool. 70: 68–73.

Silverin, B., & J. C. Wingfield. 1998. Adrenocortical responses to stress in breeding Pied Flycatchers *Ficedula hypoleuca*: relation to latitude, sex and mating status. J. Avian Biol. 29: 228–234.

Tarlow, E. M., M. Wikelski, & D. J. Anderson. 2001. Hormonal correlates of siblicide in Galapagos Nazca Boobies. Horm. Behav. 40, 14–20.

Tarlow, E. M., M. Hau, D. J. Anderson, & M. Wikelski. 2003. Diel changes in plasma melatonin and corticosterone concentrations in tropical Nazca Boobies (*Sula granti*) in relation to moon phase and age. Gen. Comp. Endocrinol.

133: 297–304.

Vallarino, A., J. C. Wingfield, & H. Drummond. 2006. Does extra corticosterone elicit increased begging and submissiveness in subordinate booby (*Sula nebouxii*) chicks? Gen. Comp. Endocrinol. 147: 297–303.

Wada, H., C. W. Breuner, J. C. Wingfield, & I. T. Moore. 2004. Stress responses in equatorial sparrows: Comparing tropical and temperate *Zonotrichia*. Integr. Comp. Biol. 44: 659–659.

Wada, H., I. T. Moore, C. W. Breuner, & J. C. Wingfield. 2006. Stress responses in tropical sparrows: Comparing tropical and temperate *Zonotrichia*. Physiol. Biochem. Zool. 79: 784–792.

Wikelski, M., M. Hau, & J. C. Wingfield. 1999. Social instability increases plasma testosterone in a year-round territorial Neotropical bird. Proc. Roy. Soc. Lond. B Biol. Sci. 266: 551–556.

Wikelski, M., M. Hau, W. D. Robinson, & J. C. Wingfield. 2003a. Reproductive seasonality of seven Neotropical passerine species. Condor 105: 683–695.

Wikelski, M., L. Spinney, W. Schelsky, A. Scheuerlein, & E. Gwinner. 2003b. Slow pace of life in tropical sedentary birds: a common-garden experiment on four Stonechat populations from different latitudes. Proc. Roy. Soc. Lond. B Biol. Sci. 270: 2383–2388.

Wilson, C. M., & R. L. Holberton. 2004. Individual risk versus immediate reproductive success: A basis for latitudinal differences in the adrenocortical response to stress in Yellow Warblers (*Dendroica petechia*). Auk 121: 1238–1249.

Wingfield, J. C., & K. E. Hunt. 2002. Arctic spring: hormone-behavior interactions in a severe environment. Comp. Biochem. Physiol. Mol. Integr. Physiol. 132: 275–286.

Wingfield, J. C., R. E. Hegner, & D. M. Lewis. 1991. Circulating levels of lutenizing-hormone and steroid-hormones in relation to social-status in the cooperatively breeding White-browed Sparrow Weaver, *Plocepasser mahali*. J. Zool. 225: 43–58.

Wingfield, J. C., R. E. Hegner, & D. M. Lewis. 1992. Hormonal responses to removal of a breeding male in the cooperatively breeding White-browed Sparrow Weaver, *Plocepasser mahali*. Horm. Behav. 26: 145–155.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. E. Lynn, M. Ramenofsky, & R. D. Richardson. 1998. Ecological bases of hormone-behavior interactions: The "emergency life history stage". Am. Zool. 38: 191–206.

Wingfield, J. C., G. Ramos-Fernandez, A. N. de la Mora, & H. Drummond. 1999. The effects of an "El Nino" southern oscillation event on reproduction in male and female Blue-footed Boobies, *Sula nebouxii*. Gen. Comp. Endocrinol. 114: 163–172.

Wingfield, J. C., S. E. Lynn, & K. K. Soma. 2001. Avoiding the 'costs' of testosterone: Ecological bases of hormone-behavior interactions. Brain Behav.Evol. 57*:* 239–251.

Wingfield, J. C., I. T. Moore, R. A. Vasquez, P. Sabat, S. Busch, A. Clark, E. Addis, R. Prado & H. Wada. 2008. Modulation of the adrenocortical responses to acute stress in northern ans southern populations of Zonotrichia. Ornitol. Neotrop. 19 (Suppl.): 241–251.