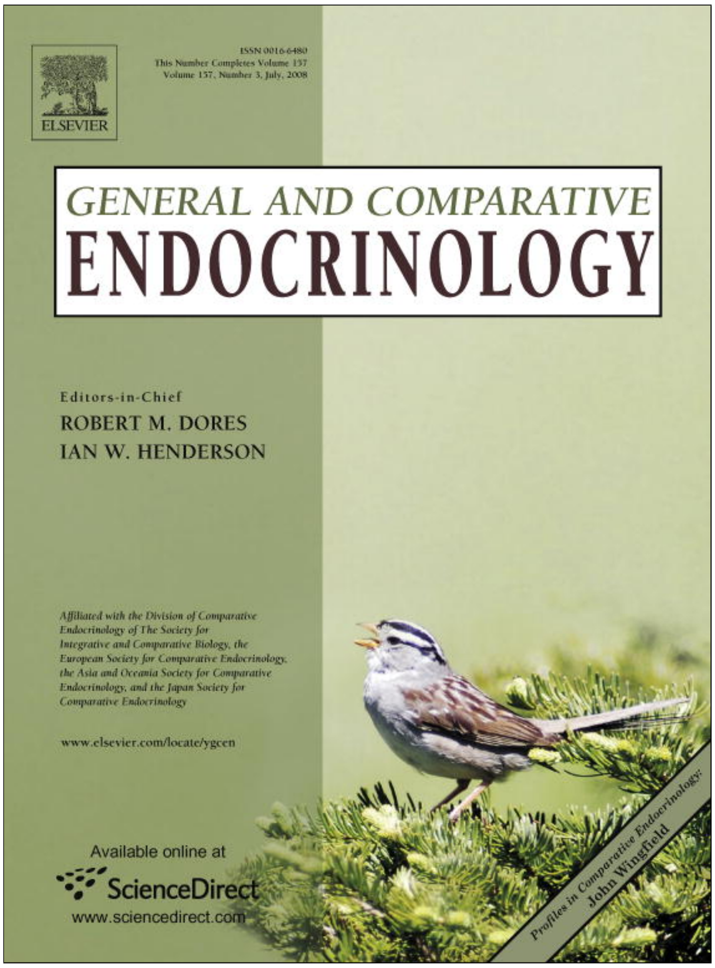

ISSN 0016-6480
This Number Completes Volume 157
Volume 157, Number 3, July, 2008

ELSEVIER

GENERAL AND COMPARATIVE
ENDOCRINOLOGY

Editors-in-Chief
ROBERT M. DORES
IAN W. HENDERSON

Affiliated with the Division of Comparative Endocrinology of The Society for Integrative and Comparative Biology, the European Society for Comparative Endocrinology, the Asia and Oceania Society for Comparative Endocrinology, and the Japan Society for Comparative Endocrinology

www.elsevier.com/locate/ygcen

Available online at
ScienceDirect
www.sciencedirect.com

Profiles in Comparative Endocrinology:
John Wingfield

General and Comparative Endocrinology 157 (2008) 241–248

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Minireview

Tropical field endocrinology: Ecology and evolution of testosterone concentrations in male birds

Michaela Hau [a,*], Sharon A. Gill [b], Wolfgang Goymann [c]

[a] Princeton University, Princeton, NJ 08540, USA
[b] Western Michigan University, Kalamazoo, MI 49008, USA
[c] Max-Planck-Institut für Ornithologie, Abteilung für Verhaltensneurobiologie, D-82319 Seewiesen, Germany

ARTICLE INFO

Article history:
Received 5 February 2008
Revised 6 May 2008
Accepted 20 May 2008
Available online 27 May 2008

Keywords:
Tropical birds
Hormone
Aggression
Territoriality
Breeding season
Social system
Mating system
Parental care
Life history
Evolutionary endocrinology

ABSTRACT

Comparative research on natural populations of vertebrates, in particular avian species, has been instrumental in documenting the existence of interspecific variation in the hormonal regulation of behavior. Studies on tropical birds, which tend to experience ecological conditions that diverge from those of higher latitude birds, have been invaluable in showcasing such variation. Here we review recent advances in tropical avian field endocrinology, focusing on male circulating testosterone concentrations during the breeding season. We summarize the evidence for a decrease in male circulating testosterone concentrations from high towards low latitudes. We revisit both established and recently proposed ecological hypotheses that attempt to explain the existence of this pattern, as well as the variation in testosterone concentrations and dynamics within tropical populations of birds. We highlight additional social and life history variables that may need to be considered if we aim at gaining an integrated understanding of the ultimate factors that influence the relationship between hormonal signals and behavioral traits in natural populations. Understanding the ecological factors that influence circulating hormone concentrations will be an important first step in our understanding of the evolutionary processes that are at the basis of variations in hormone–behavior connections. Such findings should be supplemented by studies on functional aspects of the testosterone signal at the organismal and cellular level.

1. Introduction

Animal species display vastly divergent behaviors. A central question in ecological and evolutionary endocrinology is whether the hormonal mechanisms that control behavior have diverged accordingly or whether they have remained conserved across species (Ketterson et al., 1996; Ketterson and Nolan, 1999; Hau, 2007; Adkins-Regan, 2008; Hahn and MacDougall-Shackleton, 2008; Lessells, 2008; McGlothlin and Ketterson, 2008). Answering such questions requires comparative studies that incorporate species from a wide range of ecological conditions and evolutionary histories. Birds have proven to be outstanding model systems for such research. However, though some progress has been made, avian behavioral endocrinology—like many other fields—is still biased towards northern latitude organisms (Levin and Wingfield, 1992; Stutchbury and Morton, 2001; Hau, 2001; Astheimer and Buttemer, 2002; Hau et al., 2008), largely neglecting the huge biodiversity found in the tropics (i.e., the latitudes within 23° of the equator) as well as in the southern hemisphere (e.g., Ricklefs, 2006; Hawkins et al., 2007). Ecological conditions can differ dramatically between tropical, southern hemisphere and northern latitude habitats, and populations from each region have often adopted specialized life styles and life histories. For example, many avian species from tropical and also southern hemisphere habitats are sedentary, have high survival rates and small clutch sizes, among many other characteristics (e.g., Skutch, 1949; Martin, 1996; Ricklefs, 2000). Particular avian clades diversified in the tropics (e.g., suboscine passerines), whereas others did so in temperate regions (e.g., oscine passerines; Barker et al., 2004; Hawkins et al., 2007), which might have influenced the evolution of their respective physiological organization. Hence, studying species that live outside northern latitudes allows behavioral endocrinologists to make use of an existing 'natural laboratory' to understand the ecology and evolution of endocrine control mechanisms.

Here, we will discuss recent advances in avian tropical endocrinology, specifically in our understanding of variations in seasonal patterns and maximal levels in circulating concentrations of the sex steroid testosterone. Testosterone regulates—as well as responds to—reproductive and aggressive behaviors in male vertebrates, and in many northern latitude bird species circulating concentrations of this hormone are greatly elevated during the

---

* Corresponding author. Present address: Max-Planck-Institut für Ornithologie, Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell, Germany. Fax: +49 (0) 7732 1501 69.
E-mail address: mhau@orn.mpg.de (M. Hau).

0016-6480/$ - see front matter © 2008 Published by Elsevier Inc.
doi:10.1016/j.ygcen.2008.05.008

Table 1
Environmental, social and life history variables and associated selection pressures that may contribute to low testosterone concentrations in tropical birds

Environmental/social/life history	Selection pressures
Long breeding season	Low mate competition due to low between pair synchrony
Social stability	Low rates of social conflict
Year-round territoriality	Low frequency of territorial competition
Monogamous mating system	Low reproductive competition
Long-term pair bonds	Low reproductive competition; low advertisement frequency
Low population density	Low intraspecific competition
Cooperative breeding	Low within-group aggression
Extended male paternal care	Low aggression towards offspring
Slow life history	Low reproductive rates; long life span

breeding season when males display such behaviors (Wingfield and Farner, 1993). However, the seminal work of John Wingfield has documented considerable interspecific variation in avian testosterone profiles across latitudes (summaries in Wingfield and Farner, 1993; Wingfield et al., 1997, 2000, 2001, 2006; Wingfield and Silverin, 2002). Identifying the ecological factors that determine circulating hormone concentrations is critical for understanding the evolution of hormone–behavior connections, because once in the circulation hormones can have systemic effects on various parts of the organism. Recently, studies have begun to investigate interspecific variation in responses of tissues (in particular the brain) to hormonal signals, as determined by processes such as receptor distributions sensitivities and dynamics, hormone metabolism and various other components of the hormone signaling cascade (e.g., Brenowitz, 1997; Metzdorf et al., 1999; Silverin et al., 2000; Fusani et al., 2001; Gahr, 2001; Schlinger et al., 2001; Ball et al., 2002; Soma et al., 2002; Tsutsui and Schlinger, 2002; Meddle et al., 2003; Auger, 2004; Charlier and Balthazart, 2005; Balthazart and Ball, 2006). These studies will provide important complementary information, but are still too few to put into a broader comparative framework.

In the following sections, we will review the evidence regarding a latitudinal decrease in testosterone concentrations, examine ecological factors that may account for variation in testosterone concentrations across latitudes and within the tropics, and suggest additional ecological factors that ought to be examined to increase our understanding of the selection pressures that shape hormone signals (Table 1). We will include southern hemisphere species only opportunistically as data are just beginning to accumulate (e.g., Cockrem, 1995; Buttemer and Astheimer, 2000; McDonald et al., 2001; Peters et al., 2001; Astheimer and Buttemer, 2002; Pryke et al., 2007). Furthermore, we will focus on seasonal patterns in testosterone, and not its modulation by social factors because—again—not enough is known yet about the latter in tropical species (but see, Wingfield and Lewis, 1993; Wikelski et al., 1999; Hau et al., 2004; Moore et al., 2004a; Fedy and Stutchbury, 2006; Canoine et al., 2007; Gill et al., 2008; Goymann et al., 2008). Selection pressures may differentially influence seasonally versus socially modulated secretion rates of testosterone and further study of these effects will provide additional insight into the ecology and evolution of testosterone concentrations in birds (e.g., Jawor et al., 2006, 2007; McGlothlin et al., 2007).

2. Testosterone concentrations in tropical birds

Pioneering work on afro- and neotropical birds found that males of such species have lower peak concentrations and lack the dramatic seasonal fluctuations in testosterone shown by males from northern latitudes (Dittami and Gwinner, 1985, 1990; Dittami, 1986, 1987; Dittami and Knauer, 1986; Reyer et al., 1986; Wingfield et al., 1991, 1992; Levin and Wingfield, 1992; Wingfield and Lewis, 1993; see also Krishnaprasadan et al., 1988; Narasimhacharya et al., 1988 for Asian (sub)tropical species). Recently, a comparative study that included all available data thus far confirmed the existence of a striking decrease in maximal male testosterone concentrations from high towards low latitudes (Goymann et al., 2004; Fig. 1). Males of several neotropical lowland rainforest species exemplify this finding by exhibiting almost no seasonal fluctuations in testosterone and having breeding season testosterone concentrations that are almost one order of magnitude lower than those of temperate zone species (Fig. 2a, c, and e; see also Wikelski et al., 2000; Fedy and Stutchbury, 2006; Gill et al., 2008).

Intriguingly, this comparative study (Goymann et al., 2004) also highlighted the existence of interspecific variation in peak testosterone concentrations among tropical bird species. A number of tropical species show peak concentrations of testosterone well within the range of northern latitude birds (summary in Goymann et al., 2004; see also Moore et al., 2002; Goymann and Wingfield, 2004; Chastel et al., 2005; Canoine et al., 2007; Fusani et al., 2007; see also Fig. 2b, d, and f). For example, neotropical rufous-collared sparrows (*Zonotrichia capensis*) have testosterone concentrations that are indistinguishable from those of congeneric arctic-breeding Gambel's white-crowned sparrows (*Z. leucophrys gambelii*) and north temperate Puget Sound white-crowned sparrows (*Z. leucophrys pugetensis*; Moore et al., 2002). Moreover, equatorial rufous-collared sparrows actually show a stronger response in testosterone secretion following pharmacological stimulation with gonadotropin-releasing hormone (GnRH) than the temperate congeners (Moore et al., 2002). Similarly, although afrotropical stonechats (*Saxicola torquata axillaris*) have lower testosterone concentrations than north temperate stonechats (*S. t. rubicola*) in almost all life-cycle stages, during egg-laying peak testosterone concentrations are higher than those of their northern temperate relatives (Fig. 3a; Goymann et al., 2006; see Rödl et al., 2004 for similar results on captive stonechats).

Hence, although a latitudinal cline exists in breeding season testosterone concentrations among avian species, considerable variation is also evident even within tropical species. As a result, a simplistic interpretation that all tropical birds have low levels of testosterone does not hold as a general rule (Goymann et al., 2004). In the following section, we discuss possible explanations for the diversity of testosterone levels observed in tropical species. Some of these factors have already been considered in statistical

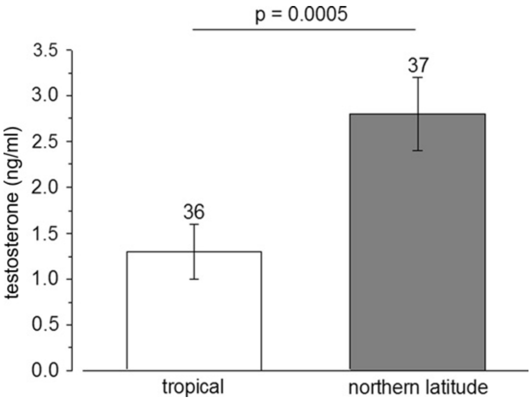

Fig. 1. Males of tropical bird species (open bar) have lower circulating concentrations of testosterone (means ± 1 SEM) during the breeding season than males of northern latitude species (filled bar; data and statistics from Goymann et al., 2004, *p*-value from phylogenetically corrected analyses). Numbers above bars refer to number of species included.

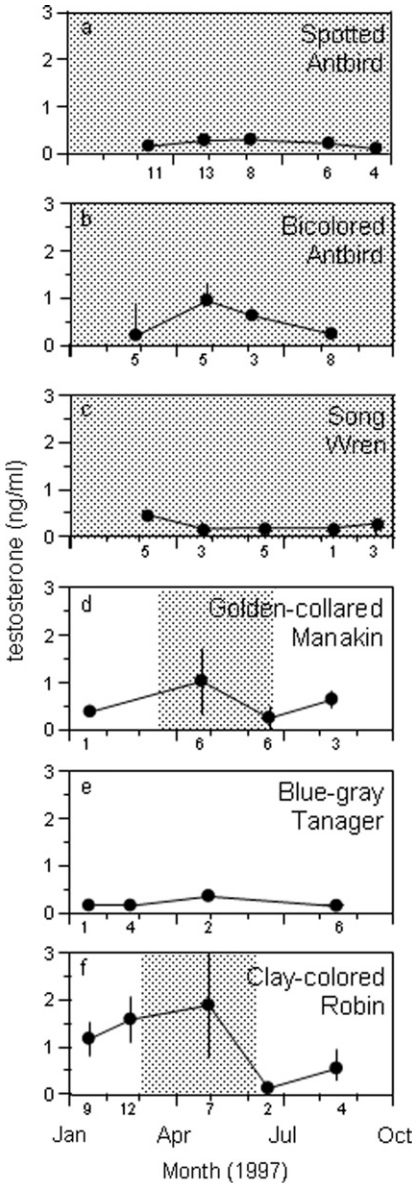

Fig. 2. Seasonal testosterone profiles (means ± SEM) of free-living males from seven bird species from central Panama (9°N), all living within about a 10-km radius. Stippled area indicates period of territoriality (modified from Wikelski et al., 2003).

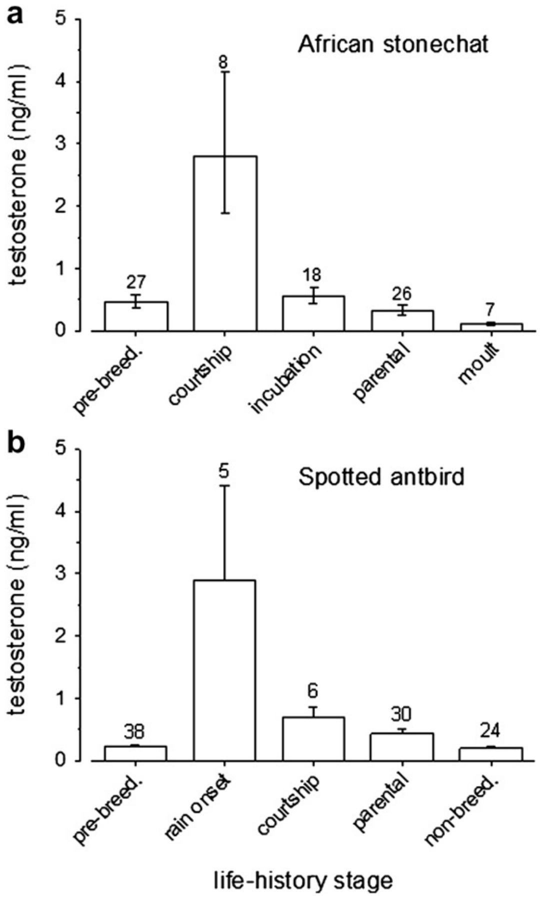

Fig. 3. Mean (±SEM) testosterone concentrations of male (a) afrotropical stonechats and (b) neotropical spotted antbirds across reproductive stages. In stonechats, testosterone concentrations were significantly higher during nest-building and egg-laying than during four other life-cycle stages ($^{*}p < 0.02$ from general linear model followed by bonferroni post hoc comparisons; data compiled from Goymann et al., 2006). In spotted antbirds, testosterone concentrations were highest at the onset of the rainy season (data compiled from Wikelski et al., 2000; Canoine et al., 2007). Numbers above bars indicate sample sizes.

analyses (Goymann et al., 2004) while others still await their inclusion in observational and experimental studies.

3. Why do male testosterone concentrations vary between latitudes, and within the tropics?

3.1. Seasonality

Often, the tropics are described as relatively stable and benign environments with little if any seasonality. This notion may be true for a few tropical ecosystems such as lowland tropical rainforests, but even the most constant tropical environments show some degree of seasonality (Baker et al., 1940). Such seasonality can be manifested in variations of climate, food abundance, predation and many other factors (e.g., Leigh et al., 1996). Seasonality may be a key ecological factor in determining testosterone concentrations: tropical species that experience pronounced seasonality exhibit peak testosterone levels similar to northern latitude species. Indeed, the length of the breeding season, which is strongly determined by seasonality, is the main predictor of testosterone levels in tropical birds according to phylogenetically controlled analyses: the shorter the breeding season the higher the testosterone concentrations of a given species (Goymann et al., 2004). Without phylogenetic control, two factors in addition to breeding season length emerged: birds that breed at high altitude have higher concentrations of testosterone than birds breeding at low altitude, and birds that establish a seasonal territory have higher concentrations of testosterone than year-round territorial or colonial species (Goymann et al., 2004). This difference in results from phylogenetically controlled versus conventional analyses is possibly due to sample size limitations, with seasonally territorial birds mainly being represented by the closely related *Fringillidae* and *Passeridae* taxa, and colonial birds mainly being represented by closely related seabird taxa. In any case, these comparisons suggest that seasonality is an important ecological variable: when tropical birds experience pronounced seasonality (short breeding seasons, breeding at higher elevations or seasonal territoriality) they show peak testosterone levels similar to northern latitude species (for example rufous-collared sparrows; Moore et al., 2002). When breeding seasons are prolonged, peak testosterone levels of tropical birds are low (Goymann et al., 2004; but see Chastel et al., 2005 for an exception to this pattern).

3.2. Population dynamics/social stability

The 'challenge hypothesis' (Wingfield et al., 1990) predicts that testosterone concentrations are most likely elevated during times of social instability, i.e., when territory boundaries are being disputed or dominance hierarchies established. In northern latitude species, social instability occurs mainly during spring when males arrive on breeding grounds following migration and establish breeding territories, leading in many species to seasonal elevations in testosterone. By contrast, in the tropics sedentariness combined with year-round territoriality is more typical (Stutchbury and Morton, 2001). In year-round territorial species, territorial competition is much less frequent and not tied to a specific season, because stable neighbor-relationships are established and may persist over several years (e.g., Freed, 1987; Greenberg and Gradwohl, 1997). Accordingly, those species may have no need to hormonally regulate territoriality and territorial advertisement but instead may express this behavior independently of circulating hormones (e.g., Adkins-Regan, 2005). Indeed, in spotted antbirds (*Hylophylax n. naevioides*; Fig. 2a), a year-round territorial species from neotropical lowland rainforests, males have low circulating concentrations of testosterone during most of the year (Wikelski et al., 1999, 2000; see also Dittami and Gwinner, 1990; Wiley and Goldizen, 2003; Fedy and Stutchbury, 2006; Gill et al., 2008).

However, even though basic territoriality may be displayed independently of testosterone in year-round territorial species, testosterone might still function to further boost aggressive behavior whenever males engage in intense territorial interactions. For example, testosterone concentrations in male spotted antbirds are generally low year-round and it has been suggested that androgen metabolism has primarily been sequestered to the brain, which could explain its low systemic concentrations (Hau et al., 2004; Canoine et al., 2007). Nevertheless, male plasma concentrations increase during high-intensity male–male encounters of long duration and manipulation of testosterone's concentrations and biological actions influence male aggressive behavior (Wikelski et al., 1999; Hau et al., 2000). Hence, in this species, testosterone may have biological effects on acute territorial aggression that are qualitatively similar to those in temperate zone species, but the temporal dynamics of its secretion and sites of metabolism and action have been altered to minimize circulating testosterone in the absence of direct challenge (Canoine et al., 2007).

The data on spotted antbirds emphasize that caution is required when trying to infer the biological actions of testosterone from seasonal patterns in circulating concentrations without further experimental studies (see also Section 1, and Goymann et al., 2007). Along the same lines, seasonally territorial high-altitude equatorial rufous-collared sparrows have generally high testosterone concentrations during the breeding season but territorial aggression seems not being modulated by testosterone: testosterone concentrations do not increase after aggressive interactions, and neither experimental testosterone administration nor the pharmacological blockage of its actions alter aggressive behavior (Moore et al., 2004a,b).

3.3. Mating system/pair bonds

In the challenge hypothesis, Wingfield and co-authors not only predicted low levels of testosterone in species with decreased male–male competition for territories, but also for species with low competition for mates (Wingfield et al., 1987, 1990). In their comparative analysis Goymann et al. (2004) suggested that many sedentary and colonial tropical species have low concentrations of testosterone because mate competition among males is relaxed due to the establishment of long-term pair bonds. Long-term pair bonds may be more common among tropical than among northern latitude species (Kunkel, 1974; Freed, 1987; Gill and Stutchbury, 2006), hence mating system dynamics may be another important factor selecting for low peak levels of testosterone in many tropical birds. In support of this idea, males of tropical species that establish long-term pair bonds have low testosterone (Wingfield et al., 1987; Goymann et al., 2004; Gill et al., 2008; Fig. 4). By contrast, males of tropical golden-collared manakins (*Manacus vitellinus*; Fig. 2d) and colonial frigatebirds (*Fregata magnificens*) compete for new mates in a lek-like system during each breeding season and show high concentrations of circulating testosterone (Wikelski et al., 2003; Chastel et al., 2005; Fusani et al., 2007). Similarly, during periods of mate advertisement following mate loss or divorce, testosterone could become elevated in species that establish long-term pair bonds, although this still needs to be tested.

3.4. Stimulation from receptive females

The slight seasonal changes in testosterone concentrations that are observed in some year-round territorial species (Wikelski et al., 2003) may not be due to competition with other males, but instead be related to male reproductive state or stimulation from receptive females (Goymann et al., 2007). Equatorial stonechats represent a good example: testosterone levels in males are low throughout the year suggesting that territorial behavior is not dependent on increases in testosterone. During the time females are most fertile, however, testosterone levels peak (Goymann et al., 2006; Fig. 3a, see also Fig. 3b). Similarly, some lekking species show testosterone peaks only during periods of courtship (Chastel et al., 2005), although in golden-collared manakins (*Manacus vitellinus*) testosterone declined within the first month after the onset of lekking even though courtship behavior remained unchanged (Fusani et al., 2007).

3.5. Sociality

Many cooperatively breeding (i.e., family living) species are found in tropical and subtropical areas (Arnold and Owens, 1999). Hormonal studies of cooperative breeders with a purely tropical distribution are rare, but the few existing studies suggest that breeding males may have lower testosterone concentrations during the breeding season compared to pair-breeding temperate species (Fig. 4; Reyer et al., 1986; Wingfield et al., 1991; H. Gwinner, unpubl. data). Low androgen concentrations have been suggested to be a mechanism to decrease male–male aggression within social groups (Levin and Wingfield, 1992; Poiani and Fletcher, 1994), with small changes in testosterone being sufficient to al-

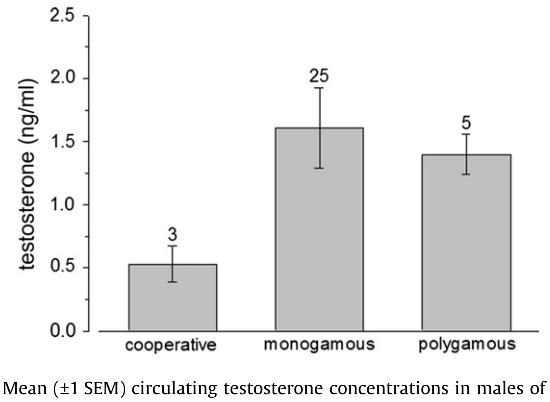

Fig. 4. Mean (±1 SEM) circulating testosterone concentrations in males of tropical bird species with cooperative, monogamous and polygamous mating systems. Numbers above bars refer to number of species included. Data were taken from Goymann et al. (2004), complemented with additional data from Chastel et al. (2005) and Fedy and Stutchbury (2006). Cooperative breeders are represented by white-browed sparrow weavers, Galapagos mockingbirds, and pied kingfishers (Reyer et al., 1986; Wingfield et al., 1991; and H. Gwinner, unpublished).

low individuals to finely adjust their responses to interactions with other males with which they have established, long-term relationships (Peters et al., 2001).

Indeed, social interactions within cooperative groups appear to influence seasonal peak testosterone concentrations. Competition between unrelated helpers and breeders for matings with breeding females results in elevated testosterone in male breeders relative to unrelated male helpers, in unrelated male helpers compared with related male helpers, and in breeding males with helpers compared with those without helpers (Reyer et al., 1986; Khan et al., 2001; Wingfield et al., 1991; Poiani and Fletcher, 1994; Vleck and Brown, 1999; Peters et al., 2001; but see Mays et al., 1991). Thus, social conflict within groups is an important determinant of testosterone concentrations. By contrast, male testosterone does not become elevated in family-living species following aggressive interactions with individuals from other social groups (Wingfield et al., 1992; Wingfield and Lewis, 1993; Gill et al., 2008). Few cooperatively breeding species have been studied so far, thus further work is needed to understand the effects of social organization on circulating testosterone concentrations.

3.6. Parental care

The challenge hypothesis proposed that testosterone levels in males of monogamous species with extensive parental care should decline when males are caring for young (Wingfield et al., 1990). Indeed in a large number of socially monogamous species from various latitudes, males show the expected seasonal decline (e.g., Silverin, 1993; Wingfield and Farner, 1993; Ketterson and Nolan, 1994; Astheimer et al., 2000; Lynn et al., 2002; Meddle et al., 2002; Van Roo et al., 2003; Van Duyse et al., 2004; see also Hirschenhauser et al., 2003). In many tropical birds, males provide considerable paternal care by incubating eggs as much as females (e.g., Auer et al., 2007), provisioning nestlings at a rate similar to females (e.g., Gill and Stutchbury, 2005), and continuing to care for young once they have fledged (Langen, 2000; Russell et al., 2004). Furthermore, a number of tropical species show periods of parental care that extend far beyond the period of offspring dependence (Willis, 1972; Langen, 2000; Russell et al., 2004; Styrsky et al., 2005). Low testosterone concentrations may be important in facilitating prolonged tolerance of males toward fledged offspring, but experimental manipulations of testosterone are needed to test this idea.

3.7. Life history/pace-of-life

Testosterone has been suggested to represent a crucial part of the physiological machinery that underlies life history strategies by mediating the trade-off between reproduction and survival (Folstad and Karter, 1992; Ketterson and Nolan, 1992; Ketterson et al., 1996; Wingfield et al., 2001; Ricklefs and Wikelski, 2002; Hau, 2007). Specifically, testosterone is known to increase male reproductive effort across vertebrate species (see Section 1), but it might do so at the expense of life span as increased circulating testosterone concentrations can decrease survival rates, immune function and other self-maintenance processes in some bird species (e.g., Dufty, 1989; Folstad and Karter, 1992; Casto et al., 2001; Wingfield et al., 2001; Reed et al., 2006; but see Roberts et al., 2004). If testosterone mediates such trade-offs, species that lie at the slow end of the 'pace-of-life continuum' with long life spans, slow development rates and low reproductive rates (for example some lowland rainforest species; Brawn et al., 1995) could be expected to have low breeding season testosterone concentrations to maximize longevity. Conversely, species with a fast pace-of-life might be able to afford higher testosterone concentrations (Hau, 2007), and may derive adaptive benefits from its performance-enhancing actions, for example on sexual and aggressive behaviors.

These ideas have not yet been explicitly tested, although comparative analyses of male testosterone concentrations in temperate and tropical species across a life history gradient are currently under way (Hau, Wikelski, Ricklefs, Lee, and Brawn, in preparation). However, experimental studies in which testosterone is administered to species exhibiting a range of life histories are needed to distinguish the above-mentioned hypothesis that testosterone mediates this trade-off across species ('evolutionary constraint hypothesis') from the alternative 'evolutionary potential hypothesis' which proposes that the actions of testosterone may vary predictably among species depending on their life history strategy (Hau, 2007). The latter hypothesis suggests that long-lived species may have evolutionarily minimized the costs of testosterone, for example by reducing (or even eliminating) the presence of androgen receptors in immune tissues, or by sequestering androgenic regulation of traits to brain tissues to avoid high systemic concentrations of testosterone (see Canoine et al., 2007). In contrast, in short-lived species testosterone might be immunosuppressive as an adaptive means to ensure the allocation of limited body resources primarily into reproductive effort instead of into self-maintenance processes (Hau, 2007). Experimental studies of testosterone-mediated trade-offs in tropical birds are currently lacking, although testosterone administration has variable effects on immune function in the few wild subtropical species studied so far (e.g., Peters, 2000; Buttemer and Astheimer, 2000; Singh and Haldar, 2005). Also, testosterone does not inhibit molt, another important self-maintenance process, in a subtropical species (Astheimer and Buttemer, 1999; although it did slow down molt in golden-collared manakins, Day et al., 2006). Interestingly, in male subtropical superb fairy wrens (*Malurus cyaneus*) testosterone even promotes prenuptial molt (Peters et al., 2000).

3.8. Probability of detection/sampling issues

Even if they exist, detecting seasonal peaks of testosterone in tropical birds may be challenging. This might be particularly true in species with prolonged breeding seasons and year-round territoriality in which breeding is much less synchronous than in seasonal species (Stutchbury and Morton, 2001). Unless the exact breeding stage of each individual bird is known, the probability of sampling males when testosterone concentrations are maximal is likely to be low. For example, male spotted antbirds have been described as having low levels of testosterone during the breeding season (Wikelski et al., 2000). Recently however, Canoine et al. (2007) found high levels of testosterone in spotted antbirds caught at the onset of the rainy season, possibly caused by a highly synchronous start of the breeding season after a prolonged dry season in that particular year (see Fig. 3b). Likewise, other tropical species have high concentrations of testosterone only for a brief period at the onset of the reproductive period (Fig. 3a; Wiley and Goldizen, 2003; Chastel et al., 2005; Goymann et al., 2006; Fusani et al., 2007). Collectively these data suggest that in a number of tropical bird species under certain circumstances the testes are capable of releasing testosterone at comparable rates than in temperate zone species. Asynchronous breeding, prolonged breeding seasons and brief transient peaks of testosterone may make it more difficult to detect the presence of high concentrations of testosterone in tropical birds compared to northern latitude species.

3.9. Phylogeny

Phylogenetic origin may contribute to seasonal patterns and maximal concentrations of testosterone in tropical birds. The extent to which phylogeny determines testosterone concentrations likely depends on the existence and strength of constraints on evolutionary changes in the testosterone production cascade (see below). If strong constraints exist, testosterone concentrations may differ predictably between major avian clades such as passerines and non-passerines or sub-oscine and oscine passerines independent of other environmental, social or life history attributes.

4. Outlook: Ecology and evolution of circulating testosterone concentrations in male birds

Because their ecologies and evolutionary histories are often different from those of higher latitude species, tropical birds are excellent models with which to further our understanding of the ecological and evolutionary factors that are at the basis of interspecific variation in circulating hormone concentrations. A latitudinal decrease in male breeding season testosterone concentrations towards low latitudes has been identified, but also the existence of considerable variation in testosterone dynamics and functions within tropical species (Goymann et al., 2004), generating ample material for future experiments.

How are low levels of testosterone physiologically accomplished in tropical birds? Or more generally, how does interspecific variation in testosterone concentrations and biological function arise on a mechanistic level? Before tackling this question one might want to consider the evolutionary histories of avian taxa. For example, within passerines suboscine and oscine clades are thought to have diverged more than 65 million years ago, with more basal clades like suboscines being more prevalent in the tropics than the derived oscines (Barker et al., 2004; Hawkins et al., 2007). This raises the possibility that such questions ought to be turned around to ask instead how northern latitude species evolved seasonally elevated circulating testosterone concentrations? Endocrine signaling pathways consist of complex cascades, with brain areas controlling the secretory activity of glands, enzymes activating or deactivating precursors or active molecules, and receptor dynamics establishing the responses of target tissues, among many other factors (Adkins-Regan, 2005, 2008). Circulating testosterone concentrations could conceivably vary interspecifically through changes in GnRH release from the hypothalamus, LH release from the pituitary, testosterone synthesis in the testes (or in other steroidogenic tissues), negative feedback of testosterone or LH on the hypothalamus, corticosterone-binding globulin availability and other possible ways (Adkins-Regan, 2005, 2008; Hau, 2007). Alternatively, temperate and tropical species might not differ in the testosterone synthesis pathway *per se*, but instead in temporal patterns of testosterone secretion (e.g., the speed of transduction of social signals, the threshold at which those signals trigger a hormonal response, the rate and pathways of hormone metabolism, etc.). This appears to be the case in several tropical species as summarized above.

Intra- and interspecific variation in steps of the testosterone-synthesis cascade is beginning to be documented (e.g., Jawor et al., 2006, 2007; Kralj-Fiser et al., 2007; Kempenaers et al., 2008), and it is this variation on which selection operates to shape circulating hormone concentrations in free-living birds. Recent research also has begun to identify possible selection pressures, responses to artificial selection, heritabilities and genetic bases of components of the testosterone production cascade (e.g., Partecke et al., 2005; Adkins-Regan, 2008; McGlothlin and Ketterson, 2008). A crucial complementary step is to understand the biological functions of testosterone signals in a similar comparative way as the hormonal signal itself, which is influenced by receptor types and dynamics, co-factors, binding globulins, and numerous other factors that mediate the cellular and organismal responses to testosterone (see Section 1). However, the fact that predictable patterns in circulating testosterone concentrations exist which can be mapped onto ecological, social and life-history variables suggest that selection does act on hormone production pathways.

Further comparative work both in the field and laboratory will be necessary to determine whether the variation in testosterone concentrations that we observe across latitudes and within the tropics is the result of exposure to different environmental or social conditions (i.e., phenotypic plasticity), phylogenetic history, evolutionary divergence and adaptation, or a combination of some or all of these factors (Hahn and MacDougall-Shackleton, 2008). Understanding the ecology and evolution of endocrine traits will be important for assessing whether populations can adapt their behaviors and life histories fast enough to cope with the rapid changes in their environment that are currently under way (Visser, 2008).

Acknowledgments

This mini-review is dedicated to John Wingfield in recognition of his pioneering work in field endocrinology. John is, and has always been, at the forefront of ecological and integrative endocrinology. We thank two anonymous reviewers for their excellent suggestions on a previous version of this manuscript. This material is based upon work supported by the National Science Foundation under Grant No. IBN-0196297 and Integrated Research Challenge Grant No. 0212587 to M.H., and by grants of the Deutsche Forschungsgemeinschaft (Go985/5-1) and the Max-Planck-Gesellschaft to W.G.

References

Adkins-Regan, E., 2005. Hormones and Animal Social Behavior. Princeton University Press, Princeton.

Adkins-Regan, E., 2008. Do hormonal control systems produce evolutionary inertia? Philos. Trans. R. Soc. Lond. B 363, 1599–1609.

Arnold, K.E., Owens, I.P.F., 1999. Cooperative breeding in birds: the role of ecology. Behav. Ecol. 10, 465–471.

Astheimer, L.B., Buttemer, W.A., 1999. Gonadal and hormonal patterns in the annual cycle of an Australian honeyeater. In: Adams, N.J., Slotow, R.H. (Eds.), Proceeding of the 22nd International Ornithology Congress BirdLife, Johannesburg, Durban, pp. 1768–1783.

Astheimer, L.B., Buttemer, W.A., 2002. Changes in latitude, changes in attitude: a perspective on ecophysiological studies of Australian birds. Emu 102, 19–27.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C., 2000. Corticosterone treatment has no effect on reproductive hormones or aggressive behavior in free-living male tree sparrows, *Spizella arborea*. Horm. Behav. 37, 31–39.

Auer, S.K., Bassar, R.D., Martin, T.E., 2007. Biparental incubation in the chestnut-vented tit-babbler *Parisoma subcaeruleum*: mates devote equal time, but males keep eggs warmer. J. Avian Biol. 38, 278–283.

Auger, A.P., 2004. Steroid receptor control of reproductive behavior. Horm. Behav. 45, 168–172.

Baker, J.R., Marshall, A.J., Harrison, T.H., 1940. The seasons in a tropical rain-forest (New Hebrides). Part 5. Birds (*Pachycephala*). J. Linn. Soc. Lond. Zool. 40, 50–71.

Ball, G.F., Riters, L.V., Balthazart, J., 2002. Neuroendocrinology of song behavior and avian brain plasticity: multiple sites of action of sex steroid hormones. Front. Neuroendocrinol. 23, 137–178.

Balthazart, J., Ball, G.F., 2006. Is brain estradiol a hormone or a neurotransmitter? Trends Neurosci. 29, 241–249.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J., Cracraft, J., 2004. Phylogeny and diversification of the largest avian radiation. Proc. Natl. Acad. Sci. USA 101, 11040–11045.

Brawn, J.D., Karr, J.R., Nichols, J.D., 1995. Demography of birds in a neotropical forest: effects of allometry, taxonomy, and ecology. Ecology 76, 41–51.

Brenowitz, E.A., 1997. Comparative approaches to the avian song system. J. Neurobiol. 33, 517–533.

Buttemer, W.A., Astheimer, L.B., 2000. Testosterone does not affect basal metabolic rate or blood parasite load in captive male White-plumed Honeyeaters *Lichenostomus penicillatus*. J. Avian Biol. 31, 479–488.

Canoine, V., Fusani, L., Schlinger, B.A., Hau, M., 2007. Low sex steroids, high steroid receptors: increasing the sensitivity of the nonreproductive brain. J. Neurobiol. 67, 57–67.

Casto, J.M., Nolan, V., Ketterson, E.D., 2001. Steroid hormones and immune function: experimental studies in wild and captive dark-eyed juncos (*Junco hyemalis*). Am. Nat. 157, 408–420.

Charlier, T.D., Balthazart, J., 2005. Modulation of hormonal signaling in the brain by steroid receptor coactivators. Rev. Neurosci. 16, 339–357.

Chastel, O., Barbraud, C., Weimerskirch, H., Lormee, H., Lacroix, A., Tostain, O., 2005. High levels of LH and testosterone in a tropical seabird with an elaborate courtship display. Gen. Comp. Endocrinol. 140, 33–40.

Cockrem, J.F., 1995. Timing of seasonal breeding in birds, with particular reference to New Zealand birds. Reprod. Fert. Dev. 7, 1–19.

Day, L.B., McBroom, J.T., Schlinger, B.A., 2006. Testosterone increases display behaviors but does not stimulate growth of adult plumage in male golden-collared manakins (*Manacus vitellinus*). Horm. Behav. 49, 223–232.

Dittami, J.P., 1986. Seasonal reproduction, moult and their endocrine correlates in two *Ploceidae* species. J. Comp. Physiol. B 156, 641–647.

Dittami, J.P., 1987. A comparison of breeding and moult cycles and life history strategies in two tropical starling species: the blue-eared glossy starling *Lamprotornis chalybaeus* and Rüppell's long-tailed glossy starling *L. purpuropterus*. Ibis 129, 69–85.

Dittami, J.P., Gwinner, E., 1985. Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. J. Zool. Lond. 207, 357–370.

Dittami, J., Gwinner, E., 1990. Endocrine correlates of seasonal reproduction and territorial behavior in some tropical passerines. In: Wada, M. (Ed.), Endocrinology of Birds: Molecular to Behavioral. Japan Sci. Soc. Press/Springer, Tokyo/Berlin, pp. 225–233.

Dittami, J., Knauer, B., 1986. Seasonal organization of breeding and molting in the Fiscal Shrike (*Lanius collaris*). J. Ornithol. 127, 79–84.

Dufty, A.M., 1989. Testosterone and survival. Horm. Behav. 23, 185–193.

Fedy, B.C., Stutchbury, B.J.M., 2006. Testosterone does not increase in response to conspecific challenges in the White-bellied antbird (*Myrmeciza longipes*), a resident tropical passerine. Auk 123, 61–66.

Folstad, I., Karter, A.J., 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139, 603–622.

Freed, L., 1987. The long-term pair bond of tropical house wrens: advantage or constraint? Am. Nat. 130, 507–525.

Fusani, L., Hutchison, J.B., Gahr, M., 2001. Testosterone regulates the activity and expression of aromatase in the canary neostriaturn. J. Neurobiol. 49, 1–8.

Fusani, L., Day, L.B., Canoine, V., Reinemann, D., Hernandez, E., Schlinger, B.A., 2007. Androgen and the elaborate courtship behavior of a tropical lekking bird. Horm. Behav. 51, 62–68.

Gahr, M., 2001. Distribution of sex steroid hormone receptors in the avian brain: functional implications for neural sex differences and sexual behaviors. Microsc. Res. Tech. 55, 1–11.

Gill, S.A., Stutchbury, B.J.M., 2005. Nest building is an indicator of parental quality in a monogamous, tropical wren *Thryothorus leucotis*. Auk 122, 1169–1181.

Gill, S.A., Stutchbury, B.J.M., 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). Behav. Ecol. Sociobiol. 61, 245–253.

Gill, S.A., Costa, L.M., Hau, M., 2008. Males if a single-brooded tropical bird species do not show increases in testosterone during social challenges. Horm. Behav. 54, 115–124.

Goymann, W., Wingfield, J.C., 2004. Competing females and caring males. Sex steroids in African black coucals, *Centropus grillii*. Anim. Behav. 68, 533–540.

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

Goymann, W., Geue, D., Schwabl, I., Flinks, H., Schmidl, D., Schwabl, H., Gwinner, E., 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., Landys, M.M., Wingfield, J.C., 2007. Distinguishing seasonal androgen responses from male–male androgen responsiveness—revisiting the challenge hypothesis. Horm. Behav. 51, 463–476.

Goymann, W., Wittenzellner, A., Schwabl, I., Makomba, M., 2008. Progesterone modulates aggression in sex-role reversed female African black coucals. Proc. R. Soc. B 275, 1053–1060.

Greenberg, R., Gradwohl, J., 1997. Territoriality, adult survival, and dispersal in the checker-throated antwren in Panama. J. Avian Biol. 28, 103–110.

Hahn, T.P., MacDougall-Shackleton, S.A., 2008. Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds. Philos. Trans. R. Soc. Lond. B 363, 267–286.

Hau, M., 2001. Timing of breeding in variable environments: tropical birds as model systems. Horm. Behav. 40, 281–290.

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

Hau, M., Wikelski, M., Soma, K.K., Wingfield, J.C., 2000. Testosterone and year-round territorial aggression in a tropical bird. Gen. Comp. Endocrinol. 117, 20–33.

Hau, M., Stoddard, S.T., Soma, K.K., 2004. Territorial aggression and hormones during the non-breeding season in a tropical bird. Horm. Behav. 45, 40–49.

Hau, M., Perfito, N., Moore, I.T., 2008. Timing of breeding in tropical birds: mechanisms and evolutionary implications. Ornithol. Neotrop. 19 (Suppl.), 39–59.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., Soeller, S.A., 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170, S16–S27.

Hirschenhauser, K., Winkler, H., Oliveira, R.F., 2003. Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. Horm. Behav. 43, 508–519.

Jawor, J.M., McGlothlin, J.W., Casto, J.M., Greives, T.J., Snajdr, E.A., Bentley, G.E., Ketterson, E.D., 2006. Seasonal and individual variation in response to GnRH challenge in male dark-eyed juncos (*Junco hyemalis*). Gen. Comp. Endocrinol. 149, 182–189.

Jawor, J.M., McGlothlin, J.W., Casto, J.M., Greives, T.J., Snajdr, E.A., Bentley, G.E., Ketterson, E.D., 2007. Testosterone response to GnRH in a female songbird varies with stage of reproduction: implications for adult behaviour and maternal effects. Funct. Ecol. 21, 767–775.

Kempenaers, B., Peters, A., Foerster, K., 2008. Sources of individual variation in plasma testosterone levels. Philos. Trans. R. Soc. Lond. B 363, 1711–1723.

Ketterson, E.D., Nolan, V., 1992. Hormones and life histories: an integrative approach. Am. Nat. 140, S33–S62.

Ketterson, E.D., Nolan, V., 1994. Male parental behavior in birds. Ann. Rev. Ecol. Syst. 25, 601–628.

Ketterson, E.D., Nolan, V., 1999. Adaptation, expatiation, and constraint: a hormonal perspective. Am. Nat. 154, S4–S25.

Ketterson, E.D., Nolan, V., Cawthorn, M.J., Parker, P.G., Ziegenfus, C., 1996. Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature. Ibis 138, 70–86.

Khan, M.Z., McNabb, F.M.A., Walters, J.R., Sharp, P.J., 2001. Patterns of testosterone and prolactin concentrations and reproductive behavior of helpers and breeders in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*). Horm. Behav. 40, 1–13.

Kralj-Fiser, S., Scheiber, I.B.R., Blejec, A., Moestl, E., Kotrschal, K., 2007. Individualities in a flock of free-roaming greylag geese: behavioral and physiological consistency over time and across situations. Horm. Behav. 51, 239–248.

Krishnaprasadan, T.N., Kotak, V.K., Sharp, P.J., Schmedemann, R., Haase, E., 1988. Environmental and hormonal factors in seasonal breeding in free-living male Indian rose-ringed parakeets (*Psitticula krameri*). Horm. Behav. 22, 488–496.

Kunkel, P., 1974. Mating systems of tropical birds: the effect of weakness or absence of external reproduction-timing factors, with special reference to prolonged pair-bonds. Z. Tierpsychol. 34, 265–307.

Langen, T., 2000. Prolonged offspring dependence and cooperative breeding in birds. Behav. Ecol. 11, 367–377.

Leigh, E.G., Rand, A.S., Windsor, D.M., 1996. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press.

Lessells, C.M., 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? Philos. Trans. R. Soc. Lond. B 363, 1589–1598.

Levin, R.N., Wingfield, J.C., 1992. The hormonal control of territorial aggression in tropical birds. Ornis Scand. 23, 284–291.

Lynn, S.E., Hayward, L.S., Benowitz-Fredericks, Z.M., Wingfield, J.C., 2002. Behavioural insensitivity to supplementary testosterone during the parental phase in the chestnut-collared longspur, *Calcarius ornatus*. Anim. Behav. 63, 795–803.

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

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

McDonald, P.G., Buttemer, W.A., Astheimer, L.B., 2001. The influence of testosterone on territorial defence and parental behavior in male free-living rufous whistlers, *Pachycephala rufiventris*. Horm. Behav. 39, 185–194.

McGlothlin, J.W., Ketterson, E.D., 2008. Hormone-mediated suites as adaptations and evolutionary constraints. Philos. Trans. R. Soc. Lond. B 363, 1611–1620.

McGlothlin, J.W., Jawor, J.M., Ketterson, E.D., 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. Am. Nat. 170, 864–875.

Meddle, S.L., Romero, L.M., Astheimer, L.B., Buttermer, W.A., Moore, I.T., Wingfield, J.C., 2002. Steroid hormone interrelationships with territorial aggression in an arctic-breeding songbird, Gambel's white-crowned sparrow, *Zonotrichia leucophrys gambelii*. Horm. Behav. 42, 212–221.

Meddle, S.L., Owen-Ashley, N.T., Richardson, M.I., Wingfield, J.C., 2003. Modulation of the hypothalamic–pituitary–adrenal axis of an Arctic-breeding polygynandrous songbird, the Smith's longspur, *Calcarius pictus*. Proc. R. Soc. Lond. B 270, 1849–1856.

Metzdorf, R., Gahr, M., Fusani, L., 1999. Distribution of aromatase, estrogen receptor, and androgen receptor mRNA in the forebrain of songbirds and nonsongbirds. J. Comp. Neurol. 407, 115–129.

Moore, I.T., Perfito, N., Wada, H., Sperry, T.S., Wingfield, J.C., 2002. Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. Gen. Comp. Endocrinol. 129, 13–19.

Moore, I.T., Wada, H., Perfito, N., Busch, D.S., Hahn, T.P., Wingfield, J.C., 2004a. Territoriality and testosterone in an equatorial population of rufous-collared sparrows, *Zonotrichia capensis*. Anim. Behav. 67, 411–420.

Moore, I.T., Walker, B.G., Wingfield, J.C., 2004b. The effects of combined aromatase inhibitor and anti-androgen on male territorial aggression in a tropical population of rufous-collared sparrows, *Zonotrichia capensis*. Gen. Comp. Endocrinol. 135, 223–229.

Narasimhacharya, A.V.R.L., Kotak, V.C., Sharp, P., 1988. Environmental and hormonal interactions in the regulation of seasonal breeding in free-living male Indian baya weaver birds (*Ploceus phillipinus*). J. Zool. Lond. 215, 239–248.

Partecke, J., Van't Hof, T.J., Gwinner, E., 2005. Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds *Turdus merula*. J. Avian Biol. 36, 295–305.

Peters, A., 2000. Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. Proc. R. Soc. Lond. B 267, 883–889.

Peters, A., Astheimer, L.B., Boland, C.R.J., Cockburn, A., 2000. Testosterone is involved in acquisition and maintenance of sexually selected male plumage in superb fairy-wrens, *Malurus cyaneus*. Behav. Ecol. Sociobiol. 47, 438–445.

Peters, A., Astheimer, L.B., Cockburn, A., 2001. The annual testosterone profile in cooperatively breeding superb fairy-wrens, *Malurus cyaneus*, reflects their extreme infidelity. Behav. Ecol. Sociobiol. 50, 519–527.

Poiani, A., Fletcher, T., 1994. Plasma levels of androgens and gonadal development of breeders and helpers in the bell miner (*Manorina melanophrys*). Behav. Ecol. Sociobiol. 34, 31–41.

Pryke, S.R., Astheimer, L.B., Buttemer, W.A., Griffith, S.C., 2007. Frequency-dependent physiological trade-offs between competing colour morphs. Biol. Lett. 3, 494–497.

Reed, W.L., Clark, M.E., Parker, P.G., Raouf, S.A., Arguedas, N., Monk, D.S., Snajdr, E., Nolan, V., Ketterson, E.D., 2006. Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. Am. Nat. 167, 667–683.

Reyer, H.-U., Dittami, J.P., Hall, M.R., 1986. Avian helpers at the nest: are they psychologically castrated? Ethology 71, 216–228.

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

Ricklefs, R.E., 2006. Global variation in the diversification rate of passerine birds. Ecology 87, 2468–2478.

Ricklefs, R.E., Wikelski, M., 2002. The physiology/life history nexus. Trends Ecol. Evol. 17, 462–468.

Roberts, M.L., Buchanan, K.L., Evans, M.R., 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. Anim. Behav. 68, 227–239.

Rödl, T., Goymann, W., Schwabl, I., Gwinner, E., 2004. Excremental androgen metabolite concentrations and gonad sizes in temperate zone vs. tropical Stonechats (*Saxicola torquata* ssp.). Gen. Comp. Endocrinol. 139, 124–130.

Russell, E.M., Yom-Tov, Y., Geffen, E., 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behav. Ecol. 15, 831–838.

Schlinger, B.A., Soma, K.K., Saldanha, C., 2001. Advances in avian behavioral endocrinology. Auk 118, 283–289.

Silverin, B., 1993. Territorial aggressiveness and its relation to the endocrine system in the pied flycatcher. Gen. Comp. Endocrinol. 89, 206–213.

Silverin, B., Baillien, M., Foidart, A., Balthazart, J., 2000. Distribution of aromatase activity in the brain and peripheral tissue of passerine and nonpasserine avian species. Gen. Comp. Endocrinol. 117, 34–53.

Singh, S.S., Haldar, C., 2005. Melatonin prevents testosterone-induced suppression of immune parameters and splenocyte proliferation in Indian tropical jungle bush quail, *Perdicula asiatica*. Gen. Comp. Endocrinol. 141, 226–232.

Skutch, A.F., 1949. Do tropical birds rear as many young as they can nourish? Ibis 91, 430–455.

Soma, K.K., Alday, N.A., Schlinger, B.A., 2002. DHEA metabolism by 3β-HSD in songbird brain: sex and regional differences. Horm. Behav. 41, 491.

Stutchbury, B.J.M., Morton, E.S., 2001. Behavioral Ecology of Tropical Birds. Academic Press, San Diego.

Styrsky, J.N., Brawn, J.D., Robinson, S.K., 2005. Juvenile mortality increases with clutch size in a neotropical bird. Ecology 86, 3238–3244.

Tsutsui, K., Schlinger, B.A., 2002. Steroidogenesis in the avian brain. In: Dawson, A., Chaturvedi, C.M. (Eds.), Avian Endocrinology. Narosa Publishing House, New Delhi, pp. 59–77.

Van Duyse, E., Pinxten, R., Darras, V.M., Arckens, L., Eens, M., 2004. Opposite changes in plasma testosterone and corticosterone levels following a simulated territorial challenge in male great tits. Behaviour 141, 451–467.

Van Roo, B.L., Ketterson, E.D., Sharp, P.J., 2003. Testosterone and prolactin in two songbirds that differ in paternal care: the blue-headed vireo and the red-eyed vireo. Horm. Behav. 44, 435–441.

Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc. R. Soc. Lond. B 275, 649–659.

Vleck, C.M., Brown, J.L., 1999. Testosterone and social and reproductive behaviour in *Aphelocoma* jays. Anim. Behav. 58, 943–951.

Wikelski, M., Hau, M., Wingfield, J.C., 1999. Social instability increases plasma testosterone in a year-round territorial neotropical bird. Proc. R. Soc. Lond. B 266, 551–556.

Wikelski, M., Hau, M., Wingfield, J.C., 2000. Seasonality of reproduction in a neotropical rain forest bird. Ecology 81, 2458–2472.

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

Wiley, C.J., Goldizen, A.W., 2003. Testosterone is correlated with courtship but not aggression in the tropical buff-banded rail, *Gallirallus philippensis*. Horm. Behav. 43, 554–560.

Willis, E.O., 1972. The behaviour of spotted antbirds. Ornithol. Monogr. 10, 1–157.

Wingfield, J.C., Farner, D.S., 1993. Endocrinology of reproduction in wild species. In: Farner, D.S., King, J.R., Parkes, K.C. (Eds.), Avian Biology, vol. IX. Harcourt Brace and Company, London, pp. 163–327.

Wingfield, J.C., Lewis, D.M., 1993. Hormonal and behavioural responses to simulated territorial intrusion in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. Anim. Behav. 45, 1–11.

Wingfield, J.C., Silverin, B., 2002. Ecophysiological studies of hormone–behavior relations in birds. In: Pfaff, D.W. (Ed.), Hormones, Brain and Behavior. Academic Press, Amsterdam, pp. 587–647.

Wingfield, J.C., Ball, G.F., Dufty, A.M., Hegner, R.E., Ramenofsky, M., 1987. Testosterone and aggression in birds. Am. Sci. 75, 602–608.

Wingfield, J.C., Hegner, R.E., Dufty, A.M., Ball, G.F., 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136, 829–846.

Wingfield, J.C., Hegner, R.E., Lewis, D.M., 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. J. Zool. Lond. 225, 43–58.

Wingfield, J.C., Hegner, R.E., Lewis, D.M., 1992. Hormonal responses to removal of a breeding male in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. Anim. Behav. 26, 145–155.

Wingfield, J.C., Jacobs, J., Hillgarth, N., 1997. Ecological constraints and the evolution of hormone–behavior interrelationships. In: Carter, S.C., Lederhendler, I.I., Kirkpatrick, B. (Eds.), The Integrative Neurobiology of Affiliation, vol. 807. New York Academy of Sciences, Washington, DC, pp. 22–41.

Wingfield, J.C., Jacobs, J.D., Tramontin, A.D., Perfito, N., Meddle, S.L., Maney, D.L., Soma, K., 2000. Toward an ecological basis of hormone–behavior interactions in reproduction of birds. In: Wallen, K., Schneider, J.E. (Eds.), Reproduction in Contexts. MIT Press, Cambridge, pp. 85–128.

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

Wingfield, J.C., Moore, I.T., Goymann, W., Wacker, D.W., Sperry, T.S., 2006. Contexts and ethology of vertebrate aggression: implications for the evolution of hormone–behavior interactions. In: Nelson, R.J. (Ed.), Biology of Aggression. Oxford University Press, Oxford, pp. 179–210.