REVIEW

Endocrine responsiveness to social challenges in northern and southern hemisphere populations of *Zonotrichia*

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Abstract Northern populations of the White-crowned Sparrow, *Zonotrichia leucophrys*, show varying degrees of social modulation of testosterone. In general, males of mid-latitude breeding and multiple-brooded populations show transient increases in secretions of luteinizing hormone and testosterone when challenged by another male for a territory, or when exposed to sexually receptive females. These surges of testosterone do not appear to activate aggression associated with territory defense or mate-guarding, but appear to enhance persistence of aggression during and after the behavioral interaction. Males may continue to sing spontaneously and patrol the territory for many hours even after the behavioral interaction is over. However, males of high latitude and altitude populations do not socially modulate testosterone levels. Several hypotheses, not necessarily mutually exclusive, have been proposed to explain why males in some populations do socially modulate testosterone and others do not. Males will not socially modulate testosterone if: (1) the breeding season is so restricted in time (e.g., high latitude and altitude) there are few social interactions; (2) populations in which males are essential for parental care; and (3) populations in which extra-pair copulations are low and male-male interactions are minimal. Tropical populations of the Rufous-collared Sparrow, *Z. capensis costaricensis*, have extended breeding seasons and they are multiple-brooded, but do not socially modulate testosterone. This is unlike *Z. leucophrys*. Whether austral populations of the Rufous-collared Sparrow socially modulate testosterone under presumably similar constraints of mid- to high-latitude seasonality are currently under investigation.

Keywords Aggression · Agonistic behavior ·
Mate guarding · Social modulation · Testosterone

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Introduction

Throughout an individual's life cycle, morphological and physiological adjustments are made in response to environmental change and are also influenced by social interactions—even in species that may spend much of their lives in isolation (Wingfield 2006). Although environmental signals may result in the activation or deactivation of appropriate behaviors (e.g., sexual behavior and territorial aggression during the reproductive season), usually through hormone signals, it is also clear that social interactions can influence responsiveness to other environmental cues and

hormone secretions (e.g., Harding 1983; Ball and Balthazart 2002; Wingfield and Silverin 2002; Adkins-Regan 2005; Wingfield 2006). Social systems and environmental change, such as seasons and unpredictable events like storms and human disturbance, interact in complex ways. What the regulatory mechanisms underlying theses interactions are, and why some populations show social modulation of hormone secretion and others do not, is an area of active theoretical analysis (e.g., Wingfield et al. 1990; Hirschenhauser et al. 2003; Goymann et al. 2004; Garamszegi et al. 2005; Hirschenhauser and Oliveira 2006).

For many species, social interactions are ubiquitous and occur throughout an organism's life cycle. These interactions include those social signals that synchronize behavioral, and physiological, traits among individuals, and integrate transitions from one behavioral state to another. This could include coordination of reproductive effort both inter- and intra-sexual, the transition from sexual to parental behavior, and precise synchronization of the behavior of a pair or group though the life cycle (Wilczynski et al. 1993; Rhen and Crews 2002; Wingfield et al. 1999a, b; Adkins-Regan 2005; Wingfield 2006). It should also be borne in mind that social plasticity (Bass and Grober 2001), social recognition and the ability to remember conspecifics (Ferguson et al. 2002) are also critical, and together the processes of social interactions impinge on all aspects of an individual's life with profound implications for neuroendocrine and endocrine control mechanisms.

Here, the focus will be on regulation of agonistic behavior related to acquisition and maintenance of a breeding territory and associated aggression related to mate guarding. Maintaining a territory is usually essential for a male to attract a female and breed successfully and in many vertebrates reproductive aggression is controlled at least in part by the steroid hormone testosterone. However, the relationship of testosterone to male aggression in the breeding season is by no means uniform, and controversy has circled this topic for decades (Harding 1983; Wingfield et al. 1990; Hirschenhauser et al. 2003; Adkins-Regan 2005; Reed et al. 2006; Wingfield 2006; Hau 2007). It is perhaps because of this controversy that the interrelationships of testosterone and aggression have been an ideal focus for the integration of theoretical approaches, from behavioral ecology, evolution and endocrinology down to cell and molecular biology.

What does testosterone do?

It is crucial to acknowledge that circulating hormones affect a complex suite of physiological, behavioral and morphological parameters simultaneously. Furthermore, combinations of effects may be restricted to specific times of year (season) or context (social) such that secretion of a particular hormone at the wrong time of year could be deleterious. Because of this, and the growing realization that organisms in the field face universal trade-offs, it is now clear that elevated plasma hormone titers can also incur costs that could reduce fitness (Ketterson et al. 1996; Wingfield et al. 1990, 1997, 2001a, b; Reed et al. 2006; Hau 2007). The steroid hormone testosterone is no exception, having a range of specific actions to regulate spermatogenesis, male reproductive associated structures, development of some secondary sex characters, muscle hypertrophy, and activation of reproductive behaviors (Wingfield 2006). In contrast, a large number of experimental studies in males show that prolonged high levels of testosterone, even within the breeding season, result in decreased expression of paternal care, increased likelihood of injury and susceptibility to predation, decreased fat stores and over winter survival, and in many cases a compromised immune system (Dufty 1989; Wingfield et al. 1990, 2001a, b; Ketterson et al. 1996; Reed et al. 2006; Hau 2007). Furthermore, high circulating levels of testosterone may also interfere with the development of the next life history stage such as molt (e.g., Runfeldt and Wingfield 1985; Schleussner and Gwinner 1988; Nolan et al. 1992).

Social modulation of testosterone and the challenge hypothesis

Although the evidence appears strong that testosterone activates aggression associated with male–male competition over territories and mates, correlations of plasma levels of testosterone with expression of territorial aggression when breeding are highly variable (Harding 1983; Ramenofsky 1984; Wingfield et al. 1990; Adkins-Regan 2005). Several explanations have been put forward, including the suggestion that baseline levels of testosterone during the breeding season are sufficient for development and maintenance of morphological, physiological and behavioral components of male reproductive function. Once the breeding season is underway, circulating testosterone concentrations do not necessarily correlate with actual expression of territorial aggression on a day-to-day or even hour-to-hour basis (Wingfield et al. 1990, 2001a, b). On a seasonal basis, testosterone titers in blood do correlate roughly with expression of territorial aggression, especially in species that are not territorial at other times of the year. However, it remained to be explained why males of some populations showed very marked correlations of testosterone levels with aggression and others did not.

A survey of the literature on testosterone and aggression in birds and mammals revealed that those studies showing a positive correlation were split about 50–50 with those

studies that found no correlation (Wingfield and Ramenofsky 1985). But most importantly, they also found that those showing a positive correlation of testosterone levels and aggression involved varying degrees of social instability, whereas those finding no correlation tended to have been conducted with animals in socially stable groups. Over the next few years, many field studies of vertebrates (now numbering over 160 species; Hirschenhauser and Oliveira 2006) revealed that circulating testosterone levels are highly plastic with transient surges leading to much higher concentrations. These surges are very often correlated with periods of heightened male–male competition. For example, plasma levels of testosterone are particularly high when establishing a territory, when challenged by another male, and when mate guarding (Wingfield et al. 1990, 1999b; Fig. 1). But this was not true of all species. Earlier analysis suggested that the reasons for this discrepancy, at least in birds, might be mating system. Males of polygynous species tended to have higher levels of testosterone for longer periods than males of socially monogamous and polyandrous species of birds (Wingfield et al. 1990)—but why?

In the 1980s, experimental manipulations of the pattern of testosterone secretion (by using subcutaneous implants of synthetic testosterone) were used to explore effects of pattern of plasma levels on aggression in male songbirds. It soon became clear that high circulating levels of testosterone for long periods may incur a "cost", such as reduced male paternal care and lower reproductive success (e.g., Silverin 1980; Hegner and Wingfield 1987). These trade-offs of testosterone and male reproductive function and costs with potentially marked effects on reproductive success have been studied in detail (for excellent reviews of the literature see: Ketterson et al. 1996; Reed et al. 2006). These led to the "challenge hypothesis" that states: high plasma levels of testosterone occur during periods of social instability in the breeding season (resulting from male–male competition for territories and mates), but are at a lower breeding baseline in stable social conditions thus allowing paternal care to be expressed (Wingfield et al. 1990a, b).

Why is there variation in the social modulation of testosterone? A phylogenetic perspective

A major confound when comparing patterns of testosterone to aggression among many species is phylogeny. It is possible that much variation in pattern of testosterone secretion may be due to phylogenetic reasons rather than ecological factors per se. In an extensive meta analysis of all avian investigations in relation to patterns of testosterone secretion and behavior, Hirschenhauser et al. (2003) tested predictions of the "trade-off" involving male–male interactions resulting in an increase of testosterone secretion and male parental care requiring a decrease in testosterone. The analysis revealed that, after adjustment for phylogeny, the overall prediction of an effect of paternal care disappeared, but the effects of mating system, male–male interactions, and possibly male participation in incubation, persisted. Testosterone patterns may vary according to mating success and testis size as well (Garamszegi et al. 2005). Hirschenhauser and Oliveira
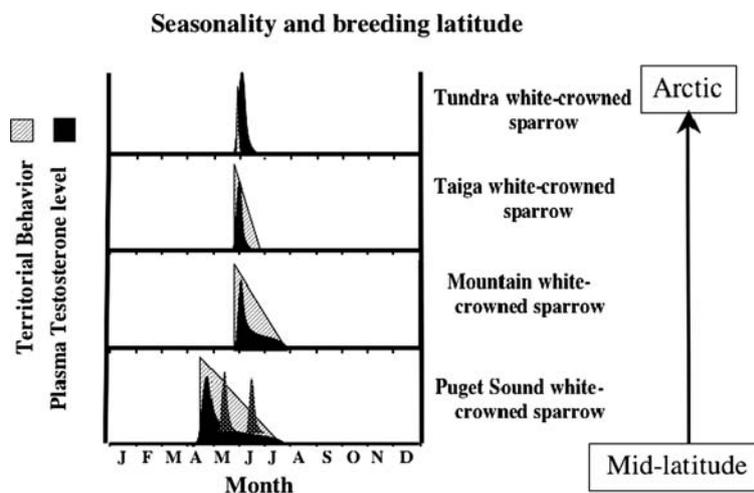

Fig. 1 A schematic diagram showing the period of territoriality (*cross hatched areas*) and plasma concentrations of testosterone (*black shapes*) in male White-crowned Sparrows, *Zonotrichia leucophrys*. The most northerly population (tundra *Z.l. gambelii*) and taiga populations of *Z.l. gambelii* have the shortest breeding season and briefest period of high testosterone levels. More southerly, multiple-brooded Puget Sound White-crowned Sparrows, *Z.l. pugetensis*, have longer breeding seasons. Only *Z.l. pugetensis* populations show social modulation of testosterone secretion (*bottom panel: two peaks with lighter shading* indicates how testosterone levels can peak after a social challenge (Wingfield and Farner 1978a, b; Wingfield and Hahn 1994; Meddle et al. 2002)

(2006) extended the meta-analyses to all vertebrates and found that tremendous variation in presence and types of parental care obscured any relationship of testosterone pattern with paternal behavior, but a general relationship with mating systems and male–male competition persisted. Thus, it appears that comparisons of patterns of testosterone secretion across multiple species upheld some of the earlier predictions of the challenge hypothesis. This is critical, because it suggests that the integration of mechanistic approaches, such as endocrinology with ecology and evolutionary biology, are not only possible, but may provide significant new insight into biodiversity of mechanisms as well as species.

We may also be able to gain additional insight into why there is variation in mechanisms of hormone action among populations. For example, for biological actions of testosterone, the evolutionary constraints hypothesis suggest that, if the mechanisms by which testosterone acts are highly conserved across all species, the pattern of secretion should be very important for adjustments to environmental and social changes (Reed et al. 2006; Hau 2007). Alternatively, the evolutionary potential hypothesis states that there may be diversity in the mechanisms by which testosterone acts at the organismal, cell and molecular levels, and multiple ways by which a suite of mechanisms may evolve in response to environmental and social change (Hau 2007). This sets the stage for many tests of these hypotheses and the exploration of biodiversity of mechanisms. Birds provide a particularly tractable model system because phylogenies for different groups are often well known, and closely related taxa have often invaded higher latitudes and altitudes independently (such as in the northern and southern hemispheres). This allows tests of the evolutionary constraints versus potential hypotheses. That is, have northern and southern populations of birds solved problems of seasonality and control of aggression patterns in reproduction by the same or different mechanisms?

Goymann et al. (2004), in a phylogenetically controlled analysis of patterns of testosterone in birds in relation to latitude and altitude, found that variable patterns in the tropics were related to environmental factors such as short breeding seasons rather than to phylogeny per se. Short breeding seasons (seasonality) tend to increase with latitude and altitude. As the numbers of species and populations studied under natural conditions increases, analyses of this sort will be critical to tease apart phylogeny and ecological constraints leading to insight into how hormone–behavior interrelationships evolved.

Field tests of the theoretical analyses above are increasing and may explain why males of some populations modulate testosterone and others do not. For example, the mid-latitude breeding subspecies of White-crowned Sparrow, *Zonotrichia leucophrys pugetensis* does socially modulate testosterone whereas the northern *Z.l. gambelii* (Fig. 1) and high altitude *Z.l. orinatha*, do not (Wingfield and Hahn 1994; Meddle et al. 2002; Lynn et al. 2007). This difference may be because the population of the latter subspecies breeds at the northern edge of the species range (68°N) on the Arctic tundra of the North Slope of Alaska. Here, the breeding season is very short and it is possible that male involvement in parental care (and reproductive success) is selected for over social modulation of testosterone. In these northern birds in general, the period of peak circulating testosterone levels is extremely brief (a day or two; Hunt et al. 1995), and males of some species may become insensitive to the effects of testosterone on aggression, possibly to ensure maximum parental effort (Hunt et al. 1997).

In a later study of the Chestnut-collared Longspur, *Calcarius ornatus*, on the high plains of Montana, males become insensitive to the effects of testosterone on aggression (i.e., implants of testosterone that restored the early spring peak concentrations failed to increase aggression; Lynn et al. 2002). Furthermore, males of this socially monogamous species do not appear to socially modulate testosterone (S. Lynn and J. Wingfield, unpublished). This species has a much longer breeding season than Arctic species and is regularly double-brooded. However, male parental care in this species appears to be essential because experimental removal of males from territories in the field resulted in complete reproductive failure (Lynn et al. 2003). This suggests that if male parental care is essential then mechanisms allowing social interactions to increase testosterone would be selected against. In a study on Snow Buntings, *Plectrophenax nivalis*, a species in which male parental care is not essential (i.e., females can compensate and raise young), experimental administration of testosterone to males in the field resulted in reduced parental care (Lynn et al. 2005). The Snow Bunting is closely related to the Longspur, minimizing the likelihood of a phylogenetic confound in this comparison.

It is also possible that other factors, such as a combination of high male parental care and degree of extra-pair copulations (Badyaev and Ghalambor 2001; Martin 2002), would influence whether males would socially modulate testosterone or not. For example, if males do show parental care and if the incidence of extra-pair copulations is low then it would be predicted that social modulation of testosterone would be selected against. This latter point has not been tested directly as yet.

Patterns of testosterone secretion in tropical birds

Most of our knowledge of physiology and endocrinology comes from northern temperate zone species. Only in the

past 20 years or so have investigations begun on tropical species where approximately 60% or more of all avian species spend at least part of their life cycles. Initially, studies on tropical species showed that males of most species had very low levels of testosterone, with some levels below the detectability of the assay systems (see Levin and Wingfield 1992; Goymann et al. 2004 for reviews). However, testicular levels of testosterone could be more similar to those of north temperate zone species, suggesting that low levels in tropical species are not the result of low production of testosterone, but the testosterone is somehow sequestered in the testis, probably by androgen binding proteins (Levin and Wingfield 1992). More intensive studies then showed that testosterone is present in some tropical species, at least at low levels (Hau et al. 2000), and is responsive to social challenge if that challenge is sustained for long enough (e.g., 2 h; Wikelski et al. 1999). Nonetheless, it seemed that tropical species generally have lower levels of testosterone than north temperate species, and that the reproductive endocrine system responded very sluggishly to social challenges (Levin and Wingfield 1992; Goymann et al. 2004).

In the late 1990s, field investigations of equatorial populations of the Rufous-collared Sparrow, Z. capensis, at around 3,300 m in elevation in Ecuador, gave contrasting insight. Males of these populations are territorial and sing mostly during the breeding season (up to 6 months), and have high circulating levels of testosterone similar to the northern White-crowned Sparrow (Fig. 2; Moore et al. 2004a). However, the pattern of testosterone levels in plasma were different from those of northern, socially monogamous songbirds, remaining elevated throughout the breeding season and showing no clear decrease during the parental phase (Moore et al. 2004a). Additionally, males from this population do not modulate testosterone levels in response to male–male interactions (Moore et al. 2004a). Moreover, treatment of free-living male Rufous-collared Sparrows with anti-androgen and an aromatase inhibitor

(to block the pathway of action of testosterone through estrogen receptors) had no effect on territorial aggression as measured by responsiveness of males to simulated territorial intrusions (Moore et al. 2004b). However, volume of song control nuclei in the brain showed seasonal changes similar to those of northern congeners (Moore et al. 2004c). These studies are fascinating because they suggest that, even within a closely related groups of populations (northern and southern Zonotrichia), mechanisms by which testosterone affects reproductive behaviors may differ markedly.

Conclusions: northern and southern comparisons, mechanisms and using closely related populations as tools

The finding that equatorial populations of the Rufous-collared sparrow have a very different pattern of testosterone secretion during the breeding season compared to northern songbirds is highly note-worthy. Furthermore, preliminary studies with chemical blockers of testosterone action suggest that expression of territorial aggression and singing behavior may not be dependent upon circulating testosterone levels. Whether or not males of populations of Rufous-collared Sparrows at southern mid- to high latitudes are more like populations of White-crowned Sparrows in similar habitats in the north is currently under investigation. A phylogeny of the Zonotrichia (Zink and Blackwell 1996) suggests that Z. capensis and Z. leucophrys are derived from a common ancestor, but the two species colonized high latitude and high altitude habitats independently. Given that the territorial behavior of the two species is very similar, this is an ideal opportunity to test whether these species regulate seasonal territorial aggression by the same mechanisms (evolutionary constraints hypothesis; Reed et al. 2006; Hau 2007) or whether they have evolved different mechanisms (evolutionary potential hypothesis; Hau 2007).

Fig. 2 Temporal patterns of territorial behavior and plasma concentrations of testosterone in male Rufous-collared Sparrows, Zonotrichia capensis costaricensis, in the Andes of Ecuador. Unpublished evidence (J.C. Wingfield, M. Wikelski, E. Hau, M. Ramenofsky and I.T. Moore) indicates a period from March to June when some males are territorial. Testosterone levels at this time remain unknown (Moore et al. 2004)
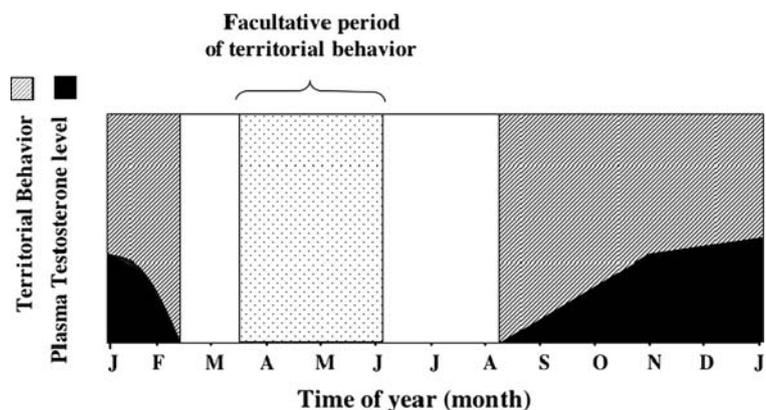
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