Testosterone in Tropical Birds: Effects of Environmental and Social Factors

Wolfgang Goymann,[1,2,*] Ignacio T. Moore,[3,†] Alexander Scheuerlein,[4,‡] Katharina Hirschenhauser,[5,§] Alan Grafen,[6,‖] and John C. Wingfield[2,#]

1. Max Planck Institute for Ornithology, Von-Der-Tann-Straße 7, D-82346 Andechs, Germany;
2. Department of Biology, University of Washington, Seattle, Washington 98195;
3. Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061–0406;
4. Department of Biology, University of Missouri, St. Louis, Missouri 63121;
5. Unidade de Investigação em Eco-Etología, Instituto Superior de Psicologia Aplicada, R. Jardim do Tabaco 34, P-1149-041 Lisbon, Portugal;
6. Zoology Department, University of Oxford, South Park Road, Oxford OX1 3PS, United Kingdom

ABSTRACT: Previous investigations suggest that male tropical birds have lower plasma testosterone concentrations than northern latitude species. To test whether this generalization is valid, we analyzed all currently available plasma testosterone data of tropical birds. We focused on peak breeding testosterone levels using phylogenetic and conventional statistics. Explanatory variables considered were social mating system, type of territoriality, breeding season length, and altitude. On average, tropical birds had lower mean peak testosterone levels than northern temperate birds. However, in several tropical species, testosterone levels were well within the range of northern latitude birds. Without controlling for phylogeny, breeding season length, type of territoriality, and altitude explained a significant proportion of the variance in testosterone levels. The shorter the breeding season, the higher the testosterone levels. Tropical birds that defend a breeding season territory had higher testosterone levels than birds that were year-round territorial or colonial, and testosterone levels were positively correlated with altitude. When controlling for phylogeny, only breeding season length predicted testosterone levels. In conclusion, we propose to refine previous notions of low plasma testosterone levels in tropical birds: short breeding seasons and perhaps environmental conditions at high altitudes precipitate conditions under which high testosterone levels are beneficial in the tropics.

Keywords: tropical birds, testosterone, length of the breeding season, territoriality, altitude.

* Corresponding author; e-mail: goymann@orn.mpg.de.

† E-mail: itmoore@vt.edu.

‡ E-mail: scheuerleina@msx.umsl.edu.

§ E-mail: k.hirschenhauser@aon.at.

‖ E-mail: alan.grafen@st-johns.oxford.ac.uk.

E-mail: jwingfie@u.washington.edu.

Previous studies have described male tropical birds as having low plasma concentrations of testosterone, involving low-amplitude cycles with possible slight elevations during times of breeding (Dittami and Gwinner 1990; Levin and Wingfield 1992; Wikelski et al. 1999a; Hau et al. 2000; Stutchbury and Morton 2001; but see Moore et al. 2002, 2004). It is thought that these low concentrations are a way of avoiding the potential detrimental effects of elevated concentrations of testosterone (Wingfield et al. 2001). Consequently, selection in the tropics may have favored birds with low concentrations of testosterone, in line with a slow pace of life, with more resources being allocated to immune function (Wikelski and Ricklefs 2001).

Previous comparative analyses of testosterone concentrations in birds were concerned with the responsiveness, that is, the magnitude of change in testosterone levels during the breeding season between different species (Wingfield et al. 1990; Hirschenhauser et al. 2003). To clarify whether tropical birds have lower concentrations of circulating testosterone than northern temperate birds it is necessary to use absolute concentrations rather than relative measures of responsiveness. The latter would generate the same results, for example, in birds with baseline and peak levels of 0.1 ng/mL and 0.4 ng/mL or 1 ng/mL and 4ng/mL, respectively, and thus would not be very useful for the purpose of this investigation.

In northern temperate birds, testosterone is typically involved in the activation of sexual behavior, mate attrac-

tion, mate guarding, and territorial aggression (Wingfield et al. 1990; Hirschenhauser et al. 2003). Thus, during periods of short-term male-male competition in a reproductive context, the persistence of male aggressiveness seems to be linked to elevated levels of testosterone. It has been suggested that year-round territoriality, common in tropical birds, is not regulated by testosterone; that year-round territorial birds are more sensitive to low plasma concentrations of testosterone (Levin and Wingfield 1992; Hau et al. 2000); and that these birds may use short-term increases to boost aggressive or sexual behavior when necessary (Wikelski et al. 1999*b*; V. Canoine and M. Hau, unpublished data). On a more functional level, Stutchbury and Morton (2001) argue that high levels of testosterone may be necessary to maintain territorial aggression, display behavior, and mate-guarding especially in species with extra-pair mating systems, which according to Stutchbury and Morton (2001) are absent in the tropics. We doubt, however, that there is sufficient information to conclude that extra-pair mating systems are less common in tropical than in temperate zone birds. Also, birds with extra-pair mating systems do not necessarily have high absolute levels of testosterone (e.g., Peters et al. 2001).

We hypothesize that even in tropical birds, testosterone concentrations can be high when the following conditions are met: first, seasonal territoriality, as the establishment of a breeding territory and seasonal competition for new mates, may be regulated by a similar physiological control mechanism as in northern temperate species; second, short breeding seasons, as high levels of a costly hormone, may be tolerable for short periods of time (Wingfield et al. 1997); and third, low environmental temperatures, as found in high altitude habitats. High altitude in the tropics corresponds to high latitude in a variety of factors (Ricklefs 1998; Poulsen 2002). High plasma levels of testosterone may induce a down-regulation in immunocompetence (an effect that is by no means ubiquitous) through either immunosuppression (Folstad and Karter 1992; Hillgarth and Wingfield 1997) or immunoredistribution (Braude et al. 1999), or through a trade-off in resource allocation between testosterone-induced and immunological traits (Wikelski and Ricklefs 2001). Hence, the costs of the effects of elevated testosterone levels should be offset in environments with a decreased number of vectors (Greiner et al. 1975) and lower developmental rates of ectoparasites (Appleton and Gouws 1996; Attenborough et al. 1997; Siziya et al. 1997). These conditions are most easily met in high altitudes in the tropics.

Methods

We reviewed the existing literature on plasma testosterone concentrations in tropical birds, defined as studies conducted within the geographical area between the tropics of Cancer (23.5°N) and Capricorn (23.5°S). For the analysis, we used breeding-season peak levels of testosterone, that is, the highest average concentrations of testosterone that have been reported in free-living and actively breeding birds of each species. Additionally, we used previously unpublished data of male birds that were collected while they were actively breeding at our own study sites in South America and Africa and additional unpublished data that were kindly provided by other researchers. We only considered species with a sample size of at least four individuals during the peak breeding season to calculate the mean plasma testosterone concentrations. In fact, seasonal profiles of a large number of individuals were available for most of the species (appendix table A1 in the online edition of the *American Naturalist*). Thus, it was unlikely that we would have missed a peak in testosterone concentrations. For cooperative breeders, only data from breeding males and not helpers were considered.

A general problem of such a comparative study is that hormone concentrations have been measured in different laboratories. Variance due to different laboratories and techniques should result in a random increase in the scatter of the data; that is, the dispersal around the "true mean" should be higher, making it more difficult to find a general pattern. Thus, any such pattern that we may find should represent a conservative estimate of any variable that may influence testosterone concentrations. In addition, we checked whether there are laboratory biases in the data. Most of the data points come from three different labs, the Wingfield laboratory (15), the Hau/Wikelski laboratory (8), and the Gwinner laboratory (7), but there was no pattern that would be explained by differences between laboratories ($F = 1.243$, df = 2, 27, $P = .304$). As a further control, we checked whether there was a correlation between the variation of testosterone and the length of the breeding season; in species with relatively long breeding seasons, peak levels of testosterone may be more likely to be missed than in species with short breeding seasons. This should result in greater variance of mean maximum testosterone concentrations in species with long breeding seasons (because at the same time some males may express peak levels whereas others do not). The result of this correlation was not significant ($r_p = -0.264$, $P = .151$), and if anything, the slope of the relationship suggests the opposite: birds with longer breeding seasons also have a lower variance in testosterone.

To our surprise, there is no review about breeding season concentrations of testosterone in northern temperate birds. We thus used the database of Hirschenhauser et al. (2003) and selected for free-ranging northern temperate birds to calculate a mean for testosterone concentrations. We then compared this mean with the mean testosterone
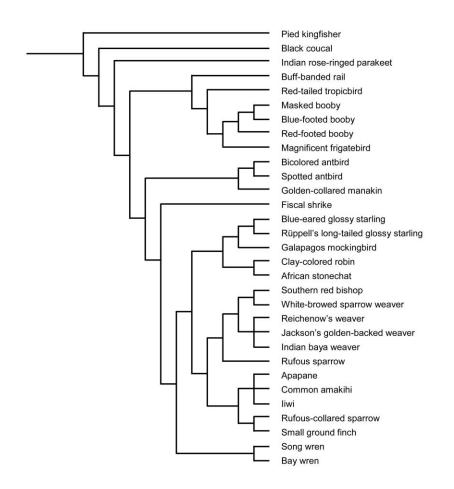
Figure 1: Phylogenetic relationship of the 31 tropical bird species included in the phylogenetic regression

concentration of the tropical birds of our data set using a conventional Mann-Whitney *U*-test and, as an alternative, phylogenetic regression (Grafen 1989). The combined phylogenetic tree for tropical and temperate birds was derived using the same sources as for tropical birds (see below).

For the analysis within tropical birds, we initially considered the following parameters for the analysis: social mating system, type of territoriality, length of the breeding season, and altitude of the breeding site. Birds were classified as monogamous if the mating system of the respective species had been described as socially monogamous. This category also includes one classically polyandrous species, the black coucal (*Centropus grillii*). We feel that the inclusion of this species in the monogamous group is justified because in a classical polyandrous system the male is mated to only one female and thus can be considered monogamous (see also Wingfield et al. 1990). However, to be conservative, we also conducted the whole analysis excluding the black coucal and got

similar results. Species that have been described as socially polygynous were classified polygynous. Birds were considered year-round territorial if they defend a multipurpose territory throughout the year, seasonal territorial if they defend a breeding territory or lekking site part of the year, and colonial if they defend only one or several nest sites in close proximity to other birds of the same species during the breeding season. The length of the breeding season and altitude were continuous variables, describing the approximate length of the breeding season in months and the elevation of the study site in meters above sea level. These parameters were subsequently eliminated from the statistical models when they turned out to be nonsignificant.

We used two kind of models to analyze the data. First, we ran a conventional general linear model with adjusted sums of squares and without controlling for phylogeny using SYSTAT 10.2 (SYSTAT, Richmond, Calif.). The initial model included type of territoriality, length of the breeding season, altitude, mating system, and an interaction be-
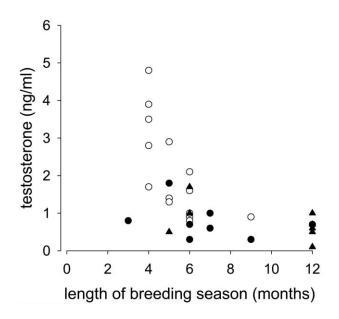
Figure 2: Length of the breeding season and testosterone in tropical bird species that are seasonal territorial (*open circles*), year-round territorial (*filled circles*), or colonial (*filled triangles*).

tween type of territoriality and length of the breeding season. The mating system was removed from the final model because it turned out to be nonsignificant. Closely related species may resemble each other in many aspects of their biology, including testosterone secretion. Thus, to control for the phylogenetic nonindependence of the data we additionally used phylogenetic regression (Grafen 1989), a method and program implemented in GLIM (Generalised Linear Interactive Modeling; Numerical Algorithms Group, Oxford) that allows testing and controlling for categorical and continuous variables. The phylogeny used for tropical birds (fig. 1) was derived from Sibley and Ahlquist (1990), with additional information from Friesen et al. (2002) and Barker et al. (2002). Branch lengths were chosen according to the arbitrary method by Grafen (1989), and tests are based on adjusted sums of squares.

Results

Published patterns of plasma testosterone concentrations in tropical birds were highly variable. The average levels (1.3 ± 0.2 ng/mL, $N = 36$; table A1) were significantly lower than those of free-ranging northern temperate birds (2.8 ± 0.4 ng/mL, $N = 37$; $U = 317.5$, $P < .0002$). The result remained similar when we controlled for phylogeny. The phylogenetically weighted mean testosterone concentrations were 1.1 ng/mL for tropical birds and 2.6 ng/mL for northern temperate birds ($F = 13.463$, df $= 1, 64$, $P < .0005$). It should be pointed out, however, that several

tropical species showed testosterone concentrations well in the range of northern temperate birds (see

Within tropical birds, the conventional general linear model without phylogenetic control found a significant effect of length of the breeding season ($F = 14.669$, df $= 1, 24$, $P = .0008$; fig. 2), type of territoriality ($F = 9.334$, df $= 2, 24$, $P = .001$; fig. 3), altitude ($F = 6.943$, df $= 1, 24$, $P = .015$; fig. 4), and the interaction between type of territoriality and length of the breeding season ($F = 7.515$, df $= 2, 24$, $P = .003$; fig. 2). The mating system was included in the initial model but removed from the final model because it did not explain a significant proportion of the variance ($F = 0.007$, df $= 1, 23$, $P = .933$).

The phylogenetic regression initially included all variables that were subsequently eliminated from the model when nonsignificant (type of territoriality: $F = 0.042$, df $= 2, 20$, $P = .96$; mating system: $F = 0.568$, df $= 1, 20$, $P = .46$; altitude: $F = 3.337$, df $= 1, 20$, $P = .083$; interaction of type of territoriality and length of the breeding season: $F = 3.201$, df $= 2, 18$, $P = .065$). The only variables that had a significant influence and were thus included in the final model were the length of the breeding season ($F = 7.443$, df $= 1, 24$, $P = .012$; fig. 2) and its quadratic term ($F = 4.884$, df $= 1, 24$, $P = .037$), indicating that there was a nonlinear component in this relationship. The shorter the breeding season, the higher the peak levels of testosterone (fig. 2).

Discussion

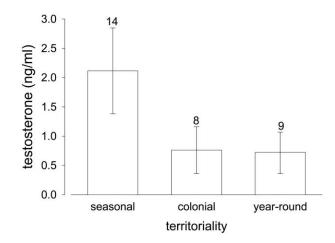On average, plasma concentrations of testosterone were lower in tropical than in northern temperate birds, thus

Figure 3: Mean testosterone concentrations ($\pm 95\%$ confidence intervals) in seasonal territorial, colonial, and year-round territorial tropical bird species (numbers above bars refer to sample size).

confirming earlier suggestions that this might be the case (Dittami and Gwinner 1990; Levin and Wingfield 1992; Wikelski et al. 1999*a*; Hau et al. 2000; Stutchbury and Morton 2001). However, low plasma concentrations of testosterone are not universal for tropical male birds because some species expressed levels that are well within the range of northern temperate birds (appendix). What are the reason for these large differences among tropical species? As reviewed by Stutchbury and Morton (2001), tropical birds are characterized by a large diversity of life-history characteristics. For example, most birds of northern latitudes defend a territory and/or mate only during a very short period of the year. In contrast, year-round territoriality and long-term pair-bonds are a common phenomenon in tropical birds, and also, the length of the breeding season is far more variable than in temperate zones (Stutchbury and Morton 2001). Also, the seasonal timing of breeding and thus the degree of population-level synchrony is more consistent across northern temperate species than across tropical species. Tropical birds are furthermore characterized by limited migration, smaller than expected clutch sizes, and longer than expected periods of parental care.

With respect to the hypotheses formulated in the introduction, both the phylogenetic regression and the conventional model suggest that the length of the breeding season is the major determinant of testosterone concentrations in tropical birds: the shorter the breeding season, the higher the testosterone maxima. This result is consistent with the hypothesis that animals avoid the costs of the effects of high sustained concentrations of testosterone (e.g., Folstad and Karter 1992; Hillgarth and Wingfield 1997; Wingfield et al. 2001). High concentrations of testosterone may be tolerable for short periods of time; and the shorter the breeding season, the higher the tolerable concentrations of this hormone (Wingfield et al. 1997). Shorter breeding seasons generally mean fewer breeding attempts, higher breeding synchrony of the population, and a greater pressure to establish and defend a territory and find a mate. Thus, the actual level of male-male competition also may be higher. These temporal constraints could have selected for individuals that, similar to northern temperate birds, have higher testosterone levels.

The other hypotheses, that seasonal territoriality and high altitude may be associated with high levels of testosterone, gain some support. In the conventional model, these variables had a significant impact; in the phylogenetic model, they represented trends that were eliminated from the final phylogenetic model. A larger number of species would be necessary to judge whether the effects of altitude and type of territoriality are spurious or true. An effect of altitude would be consistent with the idea that hormonal control mechanisms of sexual competition
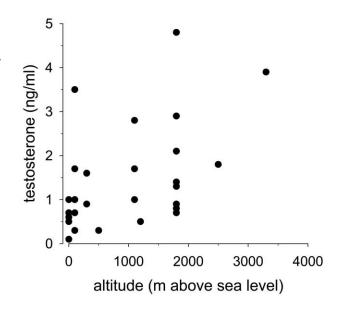

Figure 4: Elevation of the study site above sea level and testosterone concentrations.

may be similar between high-altitude tropical birds and high-latitude species (Moore et al. 2002). Furthermore, an altitudinal effect would be consistent with the immunocompetence handicap hypothesis (Folstad and Karter 1992; Hillgarth and Wingfield 1997) or the idea that there is a trade-off in resource allocation between the immunological and testosterone-induced functions (Wikelski and Ricklefs 2001); if the likelihood of parasite infections in the tropics decreases with increasing altitude (Appleton and Gouws 1996; Attenborough et al. 1997; Siziya et al. 1997), then the necessity to invest in immune function may be relieved at high altitude. Thus, tropical species at high altitude may be able to sustain higher concentrations of testosterone without compromising their immune system, while lowland tropical birds may not have this opportunity.

Sexual competition in species that establish territories, nest sites, or leks during a short period of the year (seasonal territorial birds) may be higher than in species that do not compete for new mates on a seasonal basis, such as most year-round territorial birds or the majority of colonial sea birds in our sample that establish long-term pair-bonds. That this difference only showed up in the conventional model possibly reflects the fact that most of the seasonal territorial birds with high levels of testosterone were members of the closely related families Fringillidae and Passeridae (appendix; fig. 1) and thus lack phylogenetic independence.

Life-history patterns of many Australian birds are similar to the strategies adopted by tropical birds, such as

flexible breeding schedules, limited migration, small clutch sizes, long incubation, nestling and fledgling periods, overlap between molt and breeding, and a high incidence of social cooperation (Astheimer and Buttemer 1999). Furthermore, birds of Australia have been described to have concentrations of testosterone that are one order of magnitude lower than their northern hemisphere counterparts, although there are several species with testosterone concentrations that are quite high (Astheimer and Buttemer 2002). It would be interesting to find out whether testosterone levels of Australian birds follow similar patterns as tropical species.

It is currently unknown whether the pattern of lower average concentrations of testosterone in tropical compared with northern latitude birds also exists in other vertebrate groups. Only few studies on testosterone concentrations on a latitudinal scale are available, for example, for fish, reptiles, or mammals. However, there is a large phylogenetic study comparing basal metabolic rates of small mammals along a longitudinal gradient, suggesting that basal metabolic rate is lower in tropical than in northern latitude mammals (Lovegrove 2003). Interestingly, a similar phenomenon occurs in birds: Wikelski et al. (2003*b*) found that the resting metabolic rate of tropical stonechats is significantly lower than that of stonechats of the northern temperate zones. These findings in mammals and stonechats support the "slow pace of life" hypothesis (Wikelski and Ricklefs 2001) for tropical species. In stonechats, the differences in metabolic rates are paralleled by similar differences in maximum testosterone concentrations (Rödl et al., in press). Thus, if the latitudinal changes in metabolic rates of mammals are accompanied by similar patterns in testosterone concentrations, it is possible that patterns of testosterone and latitude are similar across vertebrate taxa.

In conclusion, we propose to refine previous notions on the characteristic of low plasma testosterone in tropical birds thus: short breeding seasons and perhaps environmental conditions at high elevations that are similar to those at higher latitude result in conditions under which high testosterone levels may have evolved in the tropics. Because the length of the breeding season and the altitudinal distribution of species are phylogenetically flexible traits, we expect endocrine control mechanisms to be equally flexible on evolutionary time scales. In this regard, it would be illuminating to extend the current comparison to birds of the northern and southern temperate regions and to conduct similar analyses in other vertebrate taxa.

Acknowledgments

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