

# Testosterone in Tropical Birds: Effects of Environmental and Social Factors

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**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.

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-

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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. 1999b; 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 con-

ducted 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

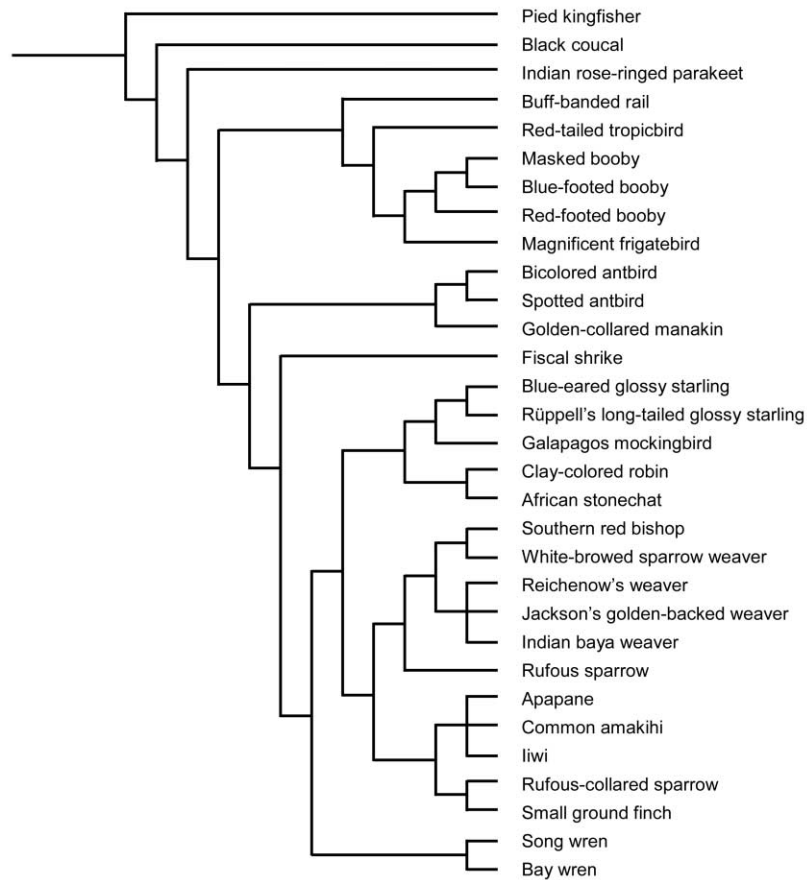


Figure 1: Phylogenetic relationship of the 31 tropical bird species included in the phylogenetic regression

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 multi-purpose 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-



confirming earlier suggestions that this might be the case (Dittami and Gwinner 1990; Levin and Wingfield 1992; Wikelski et al. 1999a; 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

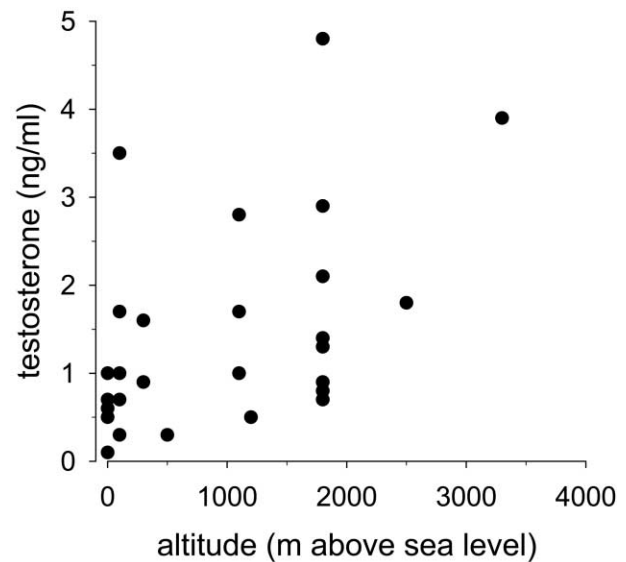


Figure 4: Elevation of the study site above sea level and testosterone concentrations.

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. (2003b) 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.

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#### Literature Cited

- Appleton, C. C., and E. Gouws. 1996. The distribution of common intestinal nematodes along an altitudinal transect in KwaZulu-Natal, South Africa. *Annals of Tropical Medicine and Parasitology* 90:181–188.
- Astheimer, L. B., and W. A. Buttemer. 1999. Gonadal and hormonal patterns in the annual cycle of an Australian honeyeater. Pages 1768–1783 in N. J. Adams and R. H. Slotow, eds. *Proceedings of the 22d International Congress of Ornithology*, Durban. BirdLife South Africa, Johannesburg.
- . 2002. Changes in latitude, changes in attitude: a perspective on ecophysiological studies of Australian birds. *Emu* 102:19–27.
- Attenborough, R. D., T. R. Burkot, and D. S. Gardner. 1997. Altitude and the risk of bites from mosquitoes infected with malaria and filariasis among the Mianmin people of New Guinea. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 91:8–10.
- Barker, K. F., G. F. Barrowclough, and J. G. Groth. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London B* 269:295–308.
- Braude, S., Z. Tang-Martinez, and G. C. Taylor. 1999. Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral Ecology* 10:345–350.
- Dittami, J. P. 1986a. A comparison of breeding and moult cycles and life histories in two tropical starling species: the blue-eared glossy starling *Lamprotornis chalybaeus* and Rueppell's long-tailed glossy starling *L. purpuropterus*. *Ibis* 129:69–85.
- . 1986b. Seasonal reproduction, moult and their endocrine correlates in two tropical Ploceidae species. *Journal of Comparative Physiology B* 156:641–647.
- Dittami, J. P., and E. Gwinner. 1985. Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *Journal of Zoology* 207:357–370.

- . 1990. Endocrine correlates of seasonal reproduction and territorial behavior in some tropical passerines. Pages 225–233 in M. Wada, ed. *Endocrinology of birds: molecular to behavioral*. Japan Scientific Society/Springer, Tokyo, Berlin.
- Dittami, J. P., and B. Knauer. 1986. Seasonal organization of breeding and molting in the Fiscal shrike, *Lanius collaris*. *Journal für Ornithologie* 127:79–84.
- Folstad, I., and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603–622.
- Friesen, V. L., D. J. Anderson, T. E. Steeves, H. Jones, and E. A. Schreiber. 2002. Molecular support for species status of the Nazca booby (*Sula granti*). *Auk* 119:820–826.
- Goymann, W., and J. C. Wingfield. In press. Competing females and caring males: sex steroids in African black coucals. *Animal Behaviour*.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society London B* 326:119–157.
- Greiner, E. C., G. F. Bennett, E. M. White, and R. F. Coombs. 1975. Distribution of the avian hematozoa of North America. *Canadian Journal of Zoology* 53:1762–1787.
- Hau, M., M. Wikelsky, K. K. Soma, and J. C. Wingfield. 2000. Testosterone and year-round territorial aggression in a tropical bird. *General and Comparative Endocrinology* 117:20–33.
- Hillgarth, N., and J. C. Wingfield. 1997. Parasite-mediated sexual selection: endocrine aspects. Pages 78–104 in D. H. Clayton and J. Moore, eds. *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford.
- Hirschenhauser, K., H. Winkler, and R. F. Oliveira. 2003. Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. *Hormones and Behavior* 43:508–519.
- Krishnaprasadan, T. N., V. C. Kotak, P. J. Sharp, R. Schmedemann, and E. Haase. 1988. Environmental and hormonal factors in seasonal breeding in free-living male Indian rose-ringed parakeets. *Hormones and Behavior* 22:488–496.
- Levin, R. N., and J. C. Wingfield. 1992. The hormonal control of territorial aggression in tropical birds. *Ornis Scandinavica* 23:284–291.
- Lormee, H., P. Jouventin, A. Lacroix, J. Lallemand, and O. Chastel. 2000. Reproductive endocrinology of tropical seabirds: sex-specific patterns in LH, steroids, and prolactin secretion in relation to parental care. *General and Comparative Endocrinology* 117:413–426.
- Lovegrove, B. G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B* 173:87–112.
- Moore, I. T., N. Perfito, H. Wada, T. S. Sperry, and J. C. Wingfield. 2002. Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. *General and Comparative Endocrinology* 129:13–19.
- Moore, I. T., H. Wada, N. Perfito, D. S. Busch, T. P. Hahn, and J. C. Wingfield. 2004. Territoriality and testosterone in an equatorial population of rufous-collared sparrows, *Zonotrichia capensis*. *Animal Behaviour* 67:411–420.
- Narasimhacharya, A. V. R. L. 1988. Environmental and hormonal interactions in the regulation of seasonal breeding in free-living male Indian baya weaver birds (*Ploceus phillipinus*). *Journal of Zoology* 215:239–248.
- Peters, A., L. B. Astheimer, and A. Cockburn. 2001. The annual testosterone profile in cooperatively breeding superb fairy-wrens, *Malurus cyaneus*, reflects their extreme infidelity. *Behavioral Ecology and Sociobiology* 50:519–527.
- Poulsen, B. O. 2002. A comparison of bird richness, abundance and trophic organization in forests of Ecuador and Denmark: are high-altitude Andean forests temperate or tropical? *Journal of Tropical Ecology* 18:615–636.
- Reyer, H. U., J. P. Dittami, and M. R. Hall. 1986. Avian helpers at the nest: are they psychologically castrated? *Ethology* 71:216–228.
- Ricklefs, R. E. 1998. Comparative demography of new world populations of thrushes (*Turdus* spp.) *Ecological Monographs* 67:23–43.
- Rödl, T., W. Goymann, I. Schwabl, and E. Gwinner. In press. Comparative analysis of gonad sizes and excreted testosterone levels in male Stonechats *Saxicola torquata* ssp. from temperate and tropical latitudes. *General and Comparative Endocrinology*.
- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and classification of birds*. Yale University Press, New Haven, Conn.
- Siziya, S., T. E. E. Watts, and P. R. Mason. 1997. Malaria in Zimbabwe: comparisons of IFAT levels, parasite and spleen rates among high, medium and lower altitude areas and between dry and rainy seasons. *Central African Journal of Medicine* 43:251–254.
- Stutchbury, B. J. M., and E. S. Morton. 2001. *Behavioral ecology of tropical birds*. Academic Press, San Diego, Calif.
- Wikelski, M., and R. E. Ricklefs. 2001. The physiology of life histories. *Trends in Ecology & Evolution* 16:479–481.
- Wikelski, M., M. Hau, W. D. Robinson, and J. C. Wingfield. 1999a. Seasonal endocrinology of tropical passerines: a comparative approach. Pages 1224–1241 in N.

- J. Adams and R. H. Slotow, eds. Proceedings of the 22d International Ornithology Congress, Durban. BirdLife South Africa, Johannesburg.
- Wikelski, M., M. Hau, and J. C. Wingfield. 1999*b*. Social instability increases plasma testosterone in a year-round territorial Neotropical bird. *Proceedings of the Royal Society of London B* 266:551–556.
- . 2000. Seasonality of reproduction in a Neotropical rain forest bird. *Ecology* 81:2458–2472.
- Wikelski, M., M. Hau, W. D. Robinson, and J. C. Wingfield. 2003*a*. Reproductive seasonality of seven Neotropical passerine bird species. *Condor* 105:683–695.
- Wikelski, M., L. Spinney, W. Schelsky, A. Scheuerlein, and E. Gwinner. 2003*b*. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B* 270:2383–2388.
- Wiley, C. J., and A. W. Goldizen. 2003. Testosterone is correlated with courtship but not aggression in the tropical buff-banded rail, *Gallirallus philippensis*. *Hormones and Behavior* 43:554–560.
- Wingfield, J. C., R. E. Hegner, A. M. Dufty, and G. F. Ball. 1990. The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist* 136:829–846.
- Wingfield, J. C., R. E. Hegner, and D. Lewis. 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *Journal of Zoology (London)* 225:43–58.
- Wingfield, J. C., J. Jacobs, and N. Hillgarth. 1997. Ecological constraints and the evolution of hormone/behavior interrelationships. *Annals of the New York Academy of Sciences* 807:22–41.
- Wingfield, J. C., G. Ramos-Fernandez, A. N. D. LaMora, and H. Drummond. 1999. The effects of an “El Niño” southern oscillation event on reproduction in male and female blue-footed boobies, *Sula nebouxii*. *General and Comparative Endocrinology* 114:163–172.
- Wingfield, J. C., S. E. Lynn, and K. K. Soma. 2001. Avoiding the “costs” of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution* 57:239–251.

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