



Hormonal correlates of social status and courtship display in the cooperatively lekking lance-tailed manakin

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ABSTRACT

Though cooperative behavior has long been a focus of evolutionary biology, the proximate hormonal mechanisms underlying cooperative interactions remain poorly understood. Lance-tailed manakins (*Chiroxiphia lanceolata*) are tropical passerines that form long-term male–male partnerships and cooperate in paired male courtship displays. To elucidate patterns of natural hormonal variation in relation to cooperation and reproductive behavior, we examined circulating androgen levels of male lance-tailed manakins in relation to social status, display behavior, and time of year. We found significantly higher circulating androgen levels in alpha-ranked (breeding) males compared to non-alpha adult males in the population. Beta males, which participated in courtship displays but did not copulate, had androgen levels indistinguishable from those of unpaired adult males that never displayed for females, suggesting that an elevated concentration of plasma testosterone in tropical lekking birds may be associated primarily with copulatory behavior or other status-specific traits, and not the performance of courtship display. Androgens decreased throughout the breeding season for males of all status categories. Interestingly, alphas that displayed for females in the observation session prior to sampling had lower androgen levels than alphas that did not display for females. This pattern may result from female discrimination against alpha males at display areas with high levels of social conflict among males, as social disruption is linked to elevated testosterone in many species. However, recent change of a display partner was not related to alpha androgen levels. We discuss alternative explanations and the possible implications of these results, and generate several testable predictions for future investigations.

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Introduction

The evolution of cooperation has long been the subject of biological inquiry, and understanding the processes that maintain cooperative interactions in complex social groups remains a critical goal of evolutionary research (Clutton-Brock, 2002). The ultimate causes of cooperation in vertebrate social systems have attracted considerable interest, but physiological mechanisms underlying this behavior are less well-studied (Soares et al., 2010). With the goal of investigating a physiological correlate of cooperative behavior, we quantified variation in circulating androgen levels among breeders, helpers, and non-helpers in males of the cooperatively displaying lance-tailed manakin (*Chiroxiphia lanceolata*). This work not only investigates the proximate mechanisms of reproductive cooperation in a novel social context, but also provides much-needed information

about androgen profiles in tropical birds (see reviews in Goymann et al., 2004; Hau et al., 2008).

Steroid hormones represent important proximate mechanisms mediating variation in many male traits. Androgens such as testosterone influence individual variation in male traits, including levels of aggression, gamete production, and avian plumage, song and display (Adkins-Regan, 2005). Testosterone has been specifically implicated in maintaining high levels of aggression and courtship display observed in systems with strong sexual selection (Hirschenhauser and Oliveira, 2006), and experimental elevation of plasma testosterone increases display behavior in at least some lekking species (Day et al., 2006). Testosterone may also be important in cooperative interactions (Eisenegger et al., 2010; Soares et al., 2010). Androgens have been implicated as a key factor that varies between dominant breeders and subordinate helpers in several cooperatively breeding species. For example, reproductively inactive subordinate males have lower testosterone concentrations than reproductively active breeding males in a variety of species, including bell miners (*Manorina melanophrys*), Florida scrub jays (*Aphelocoma coerulescens*), Seychelle warblers (*Acrocephalus sechellensis*), and white-browed sparrow weavers

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(*Plocepasser mahali*) (Brouwer et al., 2009; Poiani and Fletcher, 1994; Schoech et al., 1991, 1996; Wingfield et al., 1991). In cooperative breeders in which subordinates regularly reproduce, differences in testosterone concentrations between dominants and subordinates are less pronounced, as found in Mexican jays (*Aphelocoma ultramarina*), Harris' hawks (*Parabuteo unicinctus*) and Australian magpies (*Cracticus tibicen*), (Mays et al., 1991; Schmidt et al., 1991; Vleck and Brown, 1999). In keeping with this trend, secondary helpers in pied kingfisher (*Ceryle rudis*) groups, which are unrelated to the breeding pair and represent a reproductive threat to breeding males, have testosterone levels similar to those of breeders, whereas primary helpers, which are offspring of the breeding pair, express low levels of testosterone (Reyer et al., 1986). However, helpers of some cooperative species have levels of testosterone similar to those of breeders, even though they appear to be reproductively inactive, as in azure-winged magpies (*Cyanopica cyana*) and red-cockaded woodpeckers (*Picoides borealis*) (de la Cruz et al., 2003; Khan et al., 2001). In contrast, subordinate male superb fairy wrens (*Malurus cyaneus*) are reproductively active, but have lower levels of testosterone than dominants (Peters et al., 2001). A recent review concluded that while there are some trends in testosterone patterns of cooperative breeders, definite conclusions may be hindered by the complexity and subtle differences in the social systems summarized under the header "cooperative breeding" (Schoech et al., 2004).

Cooperative breeding is usually characterized by alloparental care of offspring (care provided by non-parental adults) (Stacey and Koenig, 1990), and therefore interpretation of androgen expression in cooperative breeders may be complicated by parental care interactions. For example, dominant breeders may not express testosterone at maximal levels throughout the breeding season, because typically males express low levels of testosterone during parental care (Wingfield et al., 1990), although this pattern is not universal (reviewed in Goymann, 2009; Lynn, 2008). Seasonal patterns of testosterone expression in non-cooperative species have similarly been attributed to conflicting demands of courtship and parental care (Chastel et al., 2005). In contrast, individuals that provide no parental care for young, such as lekking males, should demonstrate androgen profiles independent of these restrictions proposed for traditional cooperative breeders. In at least one lekking species, seasonal trends in testosterone expression are clear despite the lack of parental care (Day et al., 2006). Individuals emancipated from parental duties but that nevertheless cooperate in courtship therefore provide a useful opportunity to investigate the relationship of cooperative behavior and androgen levels. Though other studies have investigated hormonal correlates of cooperative breeding and of courtship display, this study, to our knowledge, represents the first quantification of hormone levels in a cooperatively displaying species.

Androgen levels of tropical birds have come under recent scrutiny as researchers reassess the generalization that tropical birds experience low androgen levels, even at the peak of breeding (Hau, 2001; Levin and Wingfield, 1992; Wikelski et al., 2003). Instead, recent work indicates that testosterone levels of tropical birds may peak at levels comparable to those of their temperate counterparts; and that the length of the breeding season has a strong influence on seasonal variation in circulating testosterone (Goymann et al., 2004; Hau et al., 2008). Relatively few lek-polygynous species have been studied in the tropics, with the notable exception of the golden-collared manakin (*Manacus vitellinus*). Golden-collared manakins experience elevated testosterone levels at the start of the courtship period and low testosterone in the non-breeding season, but testosterone levels fluctuate during the breeding season apparently in response to interactions with females and other males (Day et al., 2007; Fusani et al., 2007; Schlinger et al., 2008; Wikelski et al., 2003). Exogenous testosterone activates courtship display in golden-collared manakins outside the breeding season and even in females (Day et al., 2006) and treatment with androgen blockers decreases display behavior at least

for a short period of time (Fusani et al., 2007). In comparison, testosterone levels in temperate lekking species generally remain high throughout the relatively short courtship period (Alatalo et al., 1996; Mougeot et al., 2005). Male golden-collared manakins display competitively and in close proximity to one another, but courtship behavior in the manakin family ranges from solitary display to complex cooperative dances (Prum, 1994; Sick, 1967). It is unclear how trends reported in a classically lekking species may be modulated by the cooperative alliances that characterize some manakin species.

Lance-tailed manakins display for females in an exploded lek mating system, using cooperative male displays (DuVal, 2007b). Male partners form long-term alliances in which they sing duet songs and, when females are present, perform dances that involve coordinated leaps over one another and slow flight displays around the display perch on which the female sits. Males may maintain specific partnerships for up to five consecutive years (DuVal, 2007c). Adult males may be alphas (potential breeders), betas (non-breeding helpers that cooperate in courtship displays), or non-helpers (affiliate males that do not participate in courtship). Lance-tailed manakins do not maintain traditional territories, instead allowing conspecific males to enter their display area under most circumstances. Though all adult males may interact in dance and song displays when no females are present, only alphas and betas display for females, and only alpha males perform solo courtship displays or copulate. This pattern of status-specific display behavior and copulatory success has been confirmed previously through extensive observation of behavior at lek display sites, and through genetic paternity tests identifying successful sires in the study population (DuVal, 2007a; DuVal and Kempnaers, 2008).

With the goal of understanding the physiological correlates of cooperation and mate choice in the lance-tailed manakin, we first investigated how androgen levels vary among different status classes of males, exploring the potential association of courtship display or mating behavior with androgen levels. Second, we examined seasonal patterns of androgen expression, testing the hypothesis that the extended tropical breeding season results in prolonged elevation of androgens when there are no tradeoffs with parental care. Finally, we investigated how androgen levels relate to courtship display and social disruption. Although the data presented here reflect males' natural hormonal profiles, this study provides the necessary observational foundation for future manipulative work.

Materials and methods

Field methods

The study was conducted on a wild population of lance-tailed manakins found on Isla Boca Brava, Chiriquí Province, Republic of Panamá (8°12'N, 82°12'W), with the permission of local authorities and under animal care and use guidelines of the University of California, Berkeley. This site is a 46 ha area of secondary growth, dry tropical forest (<100 m above sea level). Blood samples for hormone analysis were collected from 2001 to 2003, during the breeding season (March–June) in each year; females visit male display areas and copulate throughout this time period (DuVal, 2007b).

Birds were captured with mistnets, marked with a unique combination of colored plastic leg bands, and bled for hormonal analyses. Blood samples of approximately 80 μ l were collected in heparinized capillary tubes from the brachial wing vein within 10 min of removal from the net. It is widely acknowledged that handling stress may increase circulating androgen levels, and recent evidence suggests that these changes may be more rapidly induced than previously appreciated (Deviche et al., 2010; Van Hout et al., 2010). Though time between extraction from the net and blood sampling was unrelated to androgen levels in the subset of males for which this information was recorded (mean handling time for this sample was

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