



## Testosterone, social status and parental care in a cooperatively breeding bird



Alyxandra E. Pikus<sup>a</sup>, Sarah Guindre-Parker<sup>a,b</sup>, Dustin R. Rubenstein<sup>a,c,\*</sup>

<sup>a</sup> Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA

<sup>b</sup> Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada

<sup>c</sup> Center for Integrative Animal Behavior, Columbia University, New York, NY 10027, USA

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### ABSTRACT

The steroid hormone testosterone not only plays an important role in gamete production, but also influences social and aggressive behavior. Testosterone varies seasonally, peaking when competition for mates is high and declining during parental care. Surprisingly, little is known about how testosterone mediates social conflict and parental care behavior in highly social species like cooperative breeders, where group members compete for breeding opportunities and provide parental or alloparental care. We examined how testosterone differs across breeding roles in the tropical cooperatively breeding superb starling, *Lamprotornis superbus*. We determined whether testosterone was elevated in larger groups, and whether testosterone was negatively related to total levels of parental and alloparental care. We found that male breeders had higher testosterone than male helpers and female breeders and helpers during incubation. However, breeding males exhibited a significant decline in testosterone from incubation to chick rearing, and all individuals had similar levels during the chick rearing stage. Additionally, helpers—but not breeders—in large social groups had higher testosterone than those in small groups. Finally, testosterone was not correlated with nestling provisioning rates during chick rearing, suggesting that natural variation in the low levels of testosterone observed during periods of high parental care does not affect nestling provisioning. Together, these results offer insight into how testosterone is related to breeding roles, intra-group conflict, and parental care in a highly social species.

### 1. Introduction

Testosterone is a steroid hormone that is not only critical for male spermatogenesis, but also plays a role in the development of secondary sexual characteristics—such as song and plumage among others (Lindsay et al., 2011; Van Roo, 2004; Wickings and Dixson, 1992; Wingfield et al., 1990)—suggesting that it can indirectly influence fitness (McGlothlin et al., 2010). Testosterone may also influence reproductive success due to its role in regulating aggressive behavior in both males and females during the breeding season (Hau et al., 2000; Muller and Wrangham, 2004; Sandell, 2007). Aggressive interactions often vary seasonally, typically peaking prior to mating and decreasing with the onset of parental care behavior (Wingfield et al., 1990). Testosterone follows similar seasonal patterns, reaching lowest levels during non-breeding periods and increasing during breeding for sperm production and reproduction (Hau, 2007). When intra-specific competition for mates is high, testosterone can increase above breeding levels before decreasing rapidly once mating has occurred and parental care begins. Elevated breeding testosterone is not maintained for prolonged

periods because it can be costly, leading to immune suppression and even increased mortality (Casto et al., 2000; Hau, 2001; Nolan et al., 1992; Olsson et al., 2000; Wingfield et al., 1990). Similarly, testosterone can inhibit parental care behavior such that individuals that maintain high levels of testosterone throughout offspring rearing often reduce their parental care investment, which could subsequently lead to reduced reproductive success (Horton et al., 2010; Lynn et al., 2009; Nunes et al., 2000; Rosvall, 2013; Silverin, 1980). Therefore, testosterone secretion is thought to be tightly regulated during breeding, increasing when aggressive behavior is important for reproduction but decreasing when the costs of maintaining high levels outweigh these benefits. Despite these general patterns, the role of testosterone in shaping aggression and parental care varies greatly between species, as some species may be behaviorally insensitive to the hormone (Lynn et al., 2005)—elevated testosterone is not always associated with increased aggression (Wiley and Goldizen, 2003), and the trade-off between high testosterone and reduced parental care is not observed in all species (DeVries and Jawor, 2013; Ketterson et al., 2005).

In cooperatively breeding species where both breeders (i.e. parents)

\* Corresponding author at: Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, MC5557, 1200 Amsterdam Avenue, New York, NY 10027, USA.

E-mail address: [dr2497@columbia.edu](mailto:dr2497@columbia.edu) (D.R. Rubenstein).

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and helpers (i.e. alloparents) care for young, the role of testosterone in shaping behavior remains unclear. Cooperatively breeding species are often characterized by complex social hierarchies in which one or more dominant individuals monopolize reproduction (Nelson-Flower and Ridley, 2015; Young et al., 2006). For example, in cooperatively breeding pied kingfishers, *Ceryle rudis* (Reyer et al., 1986), bell miners, *Manorina melanophrys* (Poiani and Fletcher, 1994), superb fairy wrens, *Malurus cyaneus* (Peters et al., 2001), and Florida scrub jays, *Aphelocoma c. coerulescens* (Schoech et al., 1991), dominant males have elevated testosterone relative to helper subordinate males, suggesting that testosterone is related to social status in males of these species (DuVal and Goymann, 2011; Wingfield et al., 1990). In contrast, testosterone does not differ between breeder and helper males in red-cockaded woodpeckers, *Picoides borealis* (Khan et al., 2001; Malueg et al., 2009), Harris's hawks, *Parabuteo unicinctus* (Mays et al., 1991), or Australian magpies, *Gymnorhina tibicen* (Schmidt et al., 1991). Thus, it remains unclear why testosterone levels differ between male breeding roles or with social status in some species of cooperatively breeding birds but not others.

Even less is understood about how testosterone relates to social status and influences behavior in females of cooperatively breeding species, particularly in birds. As in males, female testosterone levels in many avian species peak during the breeding season but remain low during the non-breeding season (Ketterson et al., 2005). Testosterone is secreted during pre-ovulation and is important for female reproduction as a precursor for estradiol synthesis (Johnson, 2000; Staub and De Beer, 1997). In eusocial mole-rats, *Cryptomys hottentotus natalensis* and *Fukomys damarensis*, and cooperatively breeding African cichlids, *Neolamprologus pulcher*, breeding females have been shown to have higher testosterone than helper females (Lutermann et al., 2013; Aubin-Horth et al., 2007, respectively). Testosterone has also been suggested to play a role in shaping female dominance hierarchies in other species that live in social groups, including chacma baboons, *Papio hamadryas ursinus* (Beehner et al., 2005) and spotless starlings, *Sturnus unicolor* (Veiga et al., 2004). Females in cooperatively breeding species—particularly plural cooperative breeders where multiple males and females breed per group—are as likely as males to experience elevated social conflict for access to breeding positions, mates, or nesting sites (Clutton-Brock and Huchard, 2013; Rubenstein and Lovette, 2009). Yet, very little is known about testosterone in females of cooperatively breeding bird species. Thus, testosterone may help shape both male and female breeding roles in cooperatively breeding species, though little data exist from avian species.

Although breeders in cooperatively breeding systems are often socially dominant to helpers (Clutton-Brock et al., 2004; Nelson-Flower and Ridley, 2015; Rubenstein, 2007d) and may have elevated testosterone during periods of high social conflict (Sandell, 2007; Vleck and Brown, 1999; Wingfield et al., 1990), they still invest in parental care, often to a greater degree than helpers (Carranza et al., 2008; Rubenstein, 2016; Valencia et al., 2006). Therefore, cooperatively breeding systems are useful for examining how testosterone and parental care covary because offspring care represents a mixture of both parental and alloparental care and varies widely among individuals; care may differ with breeding roles (Mumme et al., 1990; Rubenstein, 2006), among the sexes (Brouwer et al., 2014), with relatedness to the offspring (Browning et al., 2012), with individual body condition (Van de Crommenacker et al., 2011), or with environmental conditions (Wiley and Ridley, 2016). Yet, surprisingly little is known about how testosterone affects natural variation in offspring care in cooperatively breeding species. More generally, testosterone has been shown to decrease in breeders during chick rearing in both polygamous (Silverin, 1980; Wingfield, 1984) and monogamous species (Ketterson et al., 1992; Van Roo, 2004). In cooperative species, breeders may be able to reduce parental care investment compared to non-cooperative species, since alloparents may be able to compensate for reduced parental care from breeders. However, since among-group conflict in both males and

females over resources or territories, as well as within-group conflict over mates, breeding sites, or breeding roles is likely to be high in cooperative breeders (Hau et al., 2008; Peters et al., 2001; Smith et al., 2005), testosterone may be modulated differently in cooperative species during chick rearing because of the presence of alloparents. Thus, cooperatively breeding species may offer unique insight into testosterone's role in shaping male and female behaviors.

Cooperatively breeding species of birds (Jetz and Rubenstein, 2011) and mammals (Lukas and Clutton-Brock, 2017) are overwhelmingly found in tropical environments with low and variable rainfall, though studies of both tropical and cooperatively breeding species and testosterone are still rare. Seasonal changes in testosterone in tropical species are thought to be dependent upon the length of the breeding season and the degree of territoriality, as well as environmental conditions, which can differ between tropical and temperate species (Goymann et al., 2004). Here we examine how testosterone varies across breeding roles and with group size, as well as how it relates to parental care behavior, in the plural cooperatively breeding superb starling, *Lamprolaima superbus*. In this sexually monomorphic species, since multiple breeding pairs reproduce within each social group, both breeding males and females face competition for mates (Apakupakul and Rubenstein, 2015), and both sexes use song in a social context (Pilowsky and Rubenstein, 2013). First, we determined whether testosterone differed between sexes and among breeding roles in two breeding stages: prior to offspring care (i.e. incubation), when social conflict remains high due to asynchronous breeding, extra-pair mating, and mate switching; and during chick rearing, when social conflict decreases in favor of parental care, which is crucial for successfully raising young. We predicted that testosterone (1) would be higher in breeders of each sex relative to helpers because breeders are dominant to helpers in superb starlings and helpers rarely breed despite being sexually mature (Rubenstein, 2007b, 2007d), and (2) would decline in both sexes from incubation to chick rearing, when individuals shift to performing parental and alloparental care. Next, we examined how group size and the proportion of individuals breeding in a group influenced testosterone, as larger groups or the availability of breeding positions may be proxies for increased social conflict (Shen et al., 2014). We predicted that individuals in larger groups, but those with fewer breeding positions, would have higher testosterone as there may be more conflict over breeding roles when there are fewer available. Finally, we explored whether testosterone is associated with parental or alloparental care, predicting that individuals with elevated testosterone during chick rearing would provide reduced nestling care as measured by nestling provisioning rates (Hau, 2007; Wingfield et al., 1990).

## 2. Materials and methods

### 2.1. Study system

We have studied a population of free-living superb starlings at the Mpala Research Center in Laikipia, central Kenya (0°17'N, 37°52'E) since 2001. All individuals from nine social groups have been uniquely marked with a numbered metal band and a combination of four colored bands (Rubenstein, 2007a). Superb starlings breed twice per year during the short (approx. Nov–Dec) and long rainy seasons (approx. Mar–Jun). These periods have an increased availability of insects, the primary source of food delivered to nestlings (Rubenstein, 2007d; Rubenstein, 2016). Superb starlings live in plural cooperatively breeding groups of up to 50 birds where individuals care for young, either as breeders (i.e. the social parents at a nest) or helpers (i.e. subordinate individuals that guard and/or provision nestlings) (Rubenstein, 2007d). Helpers can be of either sex, and include individuals that are both related and unrelated to the breeding pairs. In addition to breeders and helpers, every breeding season some group members can forgo caring for young by taking on a non-breeding/non-helping role. Within each social group, multiple breeding pairs

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