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Clearing up the court: sex and the endocrine basis of display-court manipulation

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Sexual selection can drive the evolution of novel traits, including behaviours, that may arise in sex-specific patterns and be under sex-steroid hormone control. In some polygynous species, males actively manipulate their display environment, likely to influence female perception of male sexual traits. As a presumptive appetitive reproductive behaviour, the motivation to manipulate the display environment may be activated by reproductive hormones and the degree of motivation may vary across individuals. To evaluate these possibilities, we examined the hormone dependence of court-clearing behaviour in lek-breeding golden-collared manakins, *Manacus vitellinus*, of Panama where males clean the rainforest floor of debris within display courts and maintain these cleaned courts during the long breeding season and during subsequent years. Nonbreeding females and juvenile males were given implants containing testosterone (T) or empty (control) implants and observed in a large aviary situated in the middle of Panamanian rainforest. The aviary was planted with saplings around which males display; the bare ground was covered with dried leaves. Control-treated males removed only a few leaves from their courts. T treatment dramatically stimulated court-cleaning behaviour, including both the removal of leaves and attempts to extract small seedlings from the soil. None of the females displayed court-cleaning behaviour, although T-treated females showed low levels of some male courtship displays as well as significant levels of aggressive behaviour. To assess wild adult males' motivation to clear courts, we presented lekking males with weighted artificial leaves. Males were attentive to the leaves and motivated to remove them. With increasing weight, males utilized different methods, which often involved multiple repeated attempts to move leaves. These findings demonstrate that manakins exhibit sex-specific and hormone-dependent court-cleaning behaviours and that males are highly motivated and physically adapted to keep their courts clean.

Sexual selection, specifically female choice, is an important driver of male display behaviour and ornamentation in many taxa (West-Eberhard, 2014). Often, signals used in attraction and courtship of females exploit multiple sensory response capacities that may have been co-opted from other contexts and elaborated upon. Complex courtship displays are particularly ubiquitous in polygynous bird species, in which males often perform acrobatic routines and possess elaborate plumages (Borgia & Keagy, 2015; Prum, 1990). The diversification of sexually selected traits has been of much interest, and behavioural innovations have been proposed to lead to or facilitate changes in morphology (Mayr, 1960; West-Eberhard, 2003). The evolution of new postures or 'moves' in some bird species are known to anticipate plumage elaborations, such as long tail feathers or bright colour patches, that enhance the performance of the behaviour (Prum, 1990).

One prevalent environmental factor that may influence signalling behaviour is the display habitat (Anciães & Prum, 2008; Endler & Thery, 1996). In many polygynous birds, males perform courtship displays at a lek within a territory and typically in the same location, such as on a particular log or branch. In several species, males also actively manipulate the surrounding environment. For example, in bowerbirds (Aves: Ptilonorhynchidae), males build exquisitely ornamented bower structures that may be assessed by females and can influence female perception of male courtship

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display (Borgia & Keagy, 2015; Endler, Gaburro, & Kelley, 2014). In Neotropical manakins (Aves: Pipridae), manipulation of the display area is most elaborate in *Manacus* species, in which males clear courts on the forest floor and trim vegetation above or surrounding the court (Chapman, 1935). Clearing the display area may have several functions, including advertising court ownership and male quality to females, but it notably emphasizes plumage ornamentation and display choreography (Coccon, Schlinger, & Fusani, 2012; Uy & Endler, 2004). In the *Manacus* species hybrid zone in Panama, reflectance from court and surrounding vegetation is hypothesized to favour the introgression of the yellow collar plumage ornament into the white collar population (Uy & Stein, 2007). In several species, including *Manacus* manakins, there can be differences among individuals in display site properties, suggesting that variation exists on which selective pressures can act, such that males choose or modify their display site to improve display quality (Anciães & Prum, 2008; Uy & Stein, 2007). In manakins, manipulation of the external environment thus represents an innovation that has appeared in several unrelated taxa and which is especially conspicuous in *Manacus* species. However, to date little is known about the mechanisms that support this behaviour and that may have contributed to its appearance. To understand what influences male responses to environmental challenges, it is necessary to examine the contribution of the underlying physiological mechanisms on the performance of court cleaning.

Here, we examine court-cleaning behaviour in the golden-collared manakin, *Manacus vitellinus*. Specifically, we address the role of androgens in the activation of court cleaning and the extent that inherent motivation and muscular strength are important in its performance. Adult males that own a court at the lek engage in cleaning daily, following practice of their courtship routine when females are not observing them (Chapman, 1935). Males maintain a court during a fairly long (>6-month) breeding season and they also often return to the same court during subsequent breeding seasons. The court is approximately 50 × 50 cm and is surrounded by small vertical saplings, which are used during the typical 'jump-snap' display. During the display, males swiftly leap between saplings while performing a wing-snap, which is produced by beating their wings together above their head in midflight, and they occasionally perform a jump-snap with a half-twist landing on the ground followed by a whirring flight back onto a sapling (a 'grunt-jump' display). The court is maintained free of debris particularly at the base of the saplings as these areas may be used for landing during the grunt-jump display.

Although court cleaning involves responses to environmental inputs, it can be viewed as an appetitive reproductive behaviour and, thus, the motivation and the neuromuscular capability to perform this behaviour may be activated differently in adults under hormonal control and/or may develop uniquely across the sexes due to developmental 'organizational' events of a hormonal or genetic basis (Adkins-Regan, 2013; Arnold, 2017; Schlinger, 1998). Previous work shows that testosterone (T) activates the motivation to perform the courtship display in juvenile golden-collared manakins (Day et al., 2007; Day, McBroom, & Schlinger, 2006). Some elements of courtship are also activated by T in females, although females perform fewer male-typical behaviours and at lower rates (Chiver & Schlinger, 2017). Here, we examined whether T treatment activates court-cleaning behaviour in both sexes. In addition, we tested male motivation and muscular strength in a court-cleaning context to determine whether males vary in their performance of this behaviour. Similar to other behaviours that involve responses to unpredictable environmental conditions, such as habitat or food choice, the development of court cleaning may involve learning or prior experience (Mayr, 1974). This would be advantageous by providing flexibility in the face of variable obstacles over time and space, and may be seen as variability among males in their motivation to explore and engage in cleaning behaviour. Muscular strength in removing heavier debris may also improve with practice and males may additionally use unique motor patterns to remove heavier debris. Here, we found that (1) court-cleaning behaviour is androgen dependent; (2) testosterone activates the behaviour in males but not in females; (3) some aspects of motivation to keep the court clean vary significantly among males; (4) males possess considerable strength and can fly off carrying heavy debris (approximately their own weight) in their beaks, which is likely an adaptation to court clearing; and (5) when challenged to remove 'heavy' leaves, males exhibit some behavioural flexibility, suggesting that prior experience may be an important factor influencing court-clearing behaviour.

METHODS

Ethical Note

The work was conducted at the Smithsonian Tropical Research Institute (STRI) in Gamboa, Panama, under permits from local Panamanian authorities (Autoridad Nacional del Ambiente and MiAmbiente permits SE/A-4-14 and SE/A-55-15) and in accordance with animal care policies at STRI (Animal Care and Use Committee Protocol number 2013-0315-2016) and at the University of California Los Angeles (Office of Animal Research Oversight, ARC Protocol number 2009-123-21), which adhere to the standards set by ASAB/ABS (2012). All birds observed in captivity were released at the point of capture following the end of experiments.

Animals and Housing

To assess effects of testosterone on court-clearing behaviour, we utilized juvenile male and female golden-collared manakins, which have basal T levels and readily respond to exogenous T treatment (Chiver & Schlinger, 2017; Day et al., 2006, 2007). Wild birds were captured near leks using passive mist netting, individually marked with plastic coloured leg bands, weighed and transferred to STRI facilities in Gamboa, where they were housed individually in small cages (~36 × 29 cm and 32 cm high). Birds were in visual and auditory contact in cages set on a table in a room with open screened windows (allowing ventilation and natural lighting). Supplemental lighting was added and timed to coincide with the ambient sunrise and sunset. Fresh papaya with vitamin supplements and water were provided twice daily (ad libitum). Once three or four birds of the same sex were available, they were assigned to either a T treatment group or a control group (see below for treatment description, Treatment Administration) and transferred to a large outdoor aviary (10 × 5 m and 4.5 m tall, with a double-door entrance 1 × 1 m and 2 m tall) located ~2 km inside Soberania National Park near the town of Gamboa. The aviary contained 45 small saplings (<2 m) with straight, unbranching stems preferred by males for performing courtship displays, as well as seven trees (2–4 m tall) for perching/resting. Fresh papaya and banana slices with liquid vitamin supplement were provided at four feeders twice a day, in the morning and at midday. A water bath was provided, cleaned and refilled daily.

We conducted observations on three groups of T-treated individuals, which included two groups of females ($N = 4$ females, 9–25 October 2014; $N = 3$ females, 19 November – 9 December 2015) and one group of juvenile males ($N = 4$ males, 25 November–14 December 2014). Observations of the first T-treated group of females were terminated after 17 days because one female aggressively monopolized access to food in the aviary; observations for all other groups were terminated after 20–21 days. During the