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VIDEO ARTICLE

Sex and deception: a rare case of cheating in a lekking tropical bird

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Abstract

Many classic examples of sexually selected traits result from females making informed mate choices. Behaviors by males that increase their own reproductive success at the expense of female choice can undermine such mating systems. We documented an apparently rare example of such a behavior involving "cheating" in a facultatively cooperatively-displaying manakin species (White-ruffed manakin, *Corapipo altera*). After the cheating event, we observed a dramatic change in the behavior and activity of males displaying at the site and no subsequent female visits. We hypothesize that the infrequency of facultative cooperative behavior may in part result from cheating risks inherent in such systems. A digital video image relating to the article is available at http://www.momo-p.com/showdetail-e.php?movieid=momo190323ca01a.

Keywords Display · Male–male cooperation · Mating system · Sexual selection

Introduction

Cooperation among unrelated individuals is often viewed as an evolutionary conundrum—why forego immediate personal benefits by cooperating when selfishness can yield immediate rewards (Axelrod and Hamilton 1981)? Some unrelated cooperators relinquish mating opportunities while simultaneously increasing the reproductive success of others, but their altruistic behavior often eventually yields long-term benefits by increasing access to limited resources or enhancing social status. The cooperative mating displays of some lek-breeding Neotropical manakins (Pipridae) operate in this way (Clutton-Brock 2002; DuVal 2007a; 2013; McDonald 2007). Males of most species in this family compete for females by displaying in more-or-less aggregated courts (Prum 1990; Kirwan and Green 2012). However, the degree of cooperation varies among species. For example, in species of *Manacus*, males do not cooperate; each male displays on his own court within earshot of competitors (Snow 2004). At the other end of the spectrum, some species of *Chiroxiphia* are near-obligate cooperators; unrelated males form partnerships involving a dominant "alpha" and a subordinate "beta" which often last until one of them disappears (McDonald and Potts 1994). Synchronous vocalizations by both males attract females (Trainer and McDonald 1995; Maynard et al. 2015), and displays involve complex, coordinated maneuvers (Foster 1977; DuVal 2007b; Lukianchuk and Doucet 2014). The displays culminate in the alpha male mating with females. In *Chiroxiphia linearis*, when the alpha male dies, the beta generally assumes the new role of alpha and inherits the display site, forming a partnership with another lower-ranked male (McDonald 1989; McDonald and Potts 1994).

In species exemplifying cooperative displaying in which sexual selection operates via female choice, it seems likely that there would be strong selection on non-dominant males to sneak copulations, thereby "cheating" the dominant male. Cheating affects not only male–male alliances, but could also rob females of the power of mate choice. This could occur if females mistake the cheating male for the alpha due to the "switch" occurring out of sight of the female immediately preceding copulation. Since female choice underlies selection for male ornaments and courtship behavior in such systems, displays should converge on those in which females have control over mating decisions. In *Chiroxiphia*, the alpha male and female remain in close proximity to one another during behaviors preceding copulation, thus jointly controlling the mating context. However, the potential for such control can be more limited in other species. Male White-ruffed

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Manakins (*Corapipo altera*) facultatively display cooperatively. Some display alone, defending their courts from other males and ensuring they are the sole beneficiary of visiting female attentions. Others form alliances lasting a few months to a few years with one or more unrelated males who perform synchronous, coordinated displays alone, in the presence of other males, as well as for females (Jones et al. 2014; Jones 2017). As is typical in *Chiroxiphia*, only the dominant male copulates. When multiple males assemble at display sites, dominance hierarchies develop among the subordinates. The male immediately subordinate to the dominant male is usually the only other male to display for females (Jones et al. 2014).

Dominant male *C. altera* may have a relatively limited ability to police cooperative alliances due to the nature of their displays. Males land on the fallen, mossy log that constitutes their court, flick their wings while crouching and expanding their bright white ruffs, and fly to and fro around the log in slow, bobbing "butterfly" flights (Rosselli et al. 2002; Jones et al. 2014). Interested females approach, and when they eventually land on the log, male displays escalate in rate and intensity. The culmination takes the male far away from the female; he flies high above the canopy, circles overhead for 5–30 s giving sibilant calls, then makes a high-speed aerial dive to the log, immediately jumping and flipping around, while producing a series of vocal and/or mechanical sounds ("flap-chee-wah"). If the female has waited and is receptive, he will then immediately copulate (Jones et al. 2014). However, the dominant male's last flight above canopy level provides a window of opportunity for cheating to occur. Female *C. altera* appear to control this mating context by typically visiting display logs at times when dominant males are alone (Rosselli et al. 2002); 76.3% of displays for females involve a single male (Jones et al. 2014).

Despite the selective benefits to non-dominant males of sneaking copulations, in > 3400 h of observations of color-banded individuals at *C. altera* leks and 19,221 h of video recordings, researchers have never seen a copulation by any male other than the dominant male. Furthermore, of the > 230 articles in the Web of Knowledge database (accessed October 2017) dealing with "manakins" or "Pipridae," none explicitly reports cheating behavior despite the prevalence of intensive, observation of color-banded populations in this group. DuVal (2007a) reported genetic evidence of beta *C. lanceolata* males siring young, despite never observing cheating, and McDonald (1989) reported two copulations by a single beta male *Chiroxiphia linearis* in the absence of the alpha. In the *C. linearis* observation, although the beta may have cheated on his alpha, the female was apparently a willing partner as she had opportunity to observe the beta closely prior to copulation (McDonald 1989). Collectively, researchers have spent tens of thousands of hours observing displays of species in this family. Although it is possible that cheating events may have occurred during such observations but not documented due to observer uncertainty and lack of video footage, we suspect that such events are indeed rare in manakins; if cheating was noted or suspected during direct observations, we expect that researchers would have employed video recording more commonly and discussed possible instances of cheating in their manuscripts. Consequently, manakins appear to be unusual among cooperative taxa where theory predicts that cheating phenotypes should persist, particularly when cooperators are unrelated to one another (Van Dyken et al. 2011). Furthermore, such predictions are borne out in empirical systems ranging from bacteria (Celiker and Gore 2013) to beetles (Moczek and Emlen 2000) to fish (Fleming 1996).

Here we describe an observation of cheating in manakins which we infer to involve a male attempting to deceive both a cooperatively-displaying male and a female, and briefly discuss the implications of display behavior in the context of cheating in this system.

Observation of cheating in *Corapipo altera*

During the 2017 breeding season (March–June), we observed displays of *Corapipo altera* in Volcán Tenorio National Park in northeastern Costa Rica. We marked birds with unique color-band combinations, allowing individual recognition. We observed one of the display logs for three 2-h periods in late March and early April. Activity was always exceptionally high at this log relative to other logs in this population and others we have studied (Jones et al. 2014). We typically observed > 7 males (and a minimum of 5 adult-plumaged males) displaying and interacting during each observation. No females visited during the first three observations. This log was not what we would characterize as a "practice log," i.e., sites facultatively used by typically two to three younger (immature-plumaged) males. Although young males visited the area near the log, three adult-plumaged males were observed during at least two of the three observations early in the breeding season, and these males performed a majority of display behaviors at the log and did not interact aggressively with each other. Notably, due to the high activity at the log, our assignments of rank to the most active males were not consistent from observation to observation. However, the consistent identity of these males and the predominance of adult activity makes us confident that this log constituted a display site characterized by stable, non-aggressive male-male alliances with consistently high display activity.

On 23 April 2017 beginning at 0940 hours we observed this log from a camouflaged blind located 8 m from the display log while simultaneously recording behavior with a Canon HD VIXIA HFR700 video camera (Canon Inc., Tokyo, Japan) (Fig. 1, http://www.momo-p.com/showdetail-e.php?movieid=momo190323ca01a). For the first 35 min, activity was similar to that observed previously, with five color-banded adult males known to be associated with the log observed displaying. At 1015 hours, a female landed on the log and a sixth banded male (RB-BS) began a solo display for the female characteristic of a dominant male, while the other males that had previously been active at the log stopped all display behavior but remained in close proximity to the display area. This "presumed alpha" male displayed animatedly for 20 s until he was briefly interrupted by another male (bands not seen) who he chased in an aggressive pursuit (Jones et al. 2014). RB-BS returned and immediately resumed displaying for the female who had remained on the log during the interruption in display. Thirty-five seconds later, RB-BS flew above the canopy to commence the final portion of the display. As is typical of a receptive female, the female visitor remained on the log during the above-canopy portion of the male display. Roughly 25 s later, an unknown adult male (bands not seen) flew to a branch a few meters above and behind the female and log. It is possible that this male was the one that had been aggressively chased by the alpha, or it could have been one of the five males engaged in cooperative display as none of the other males in the vicinity of the log acted aggressively toward this male. We cannot be sure if this male was perched out of sight of the female, but it seems possible given that the female was oriented with her back to the male's perch location. It is common for subordinate males to remain nearby while alpha males complete their displays and copulate with females, so the presence of another male may not have elicited a response by the female if she did notice his presence. This unknown male then dropped down next to the female as if in the final aerial dive of the flap-chee-wah display and attempted to mount the female to copulate. As that male dropped down, the female turned to face him at the last moment and appeared to begin moving away. Almost simultaneously, RB-BS completed his dive, knocked the cheater off the female, and both the female and the cheater flew off. Immediately thereafter, all other subordinates in the area flew away and were not seen again for the remaining 1.5 h. RB-BS remained near the log but did not display again. The cheating event and the change in social interactions following the event were strikingly obvious to the in-person observer and would have been detected in the absence of video evidence. However, we also documented and were able to review the sequence on the digital video image accompanying this article (Fig. 1, http://www.momo-p.com/showdetail-e.php?movieid=momo190323ca01a).

Fig. 1 Video clip (VideoFigure1.mov; file size 129 MB) documenting cheating by a male white-ruffed manakin. Recording made at Volcán Tenorio National Park in Costa Rica on 23 April 2017. First, the dominant male displays by doing butterfly flights and log landings for the female who is present on the log from the start. At 0:00:33, the dominant male flies off camera to above the canopy where he circles and calls for 25 s. At 0:00:57, the cheater flies to a perch above the female, then drops to the log and attempts to copulate (0:01:00) before being forced off her by the diving dominant male immediately afterward. Following the full, unedited clip, we repeat key points in this sequence at 30% of the original speed. http://www.momo-p.com/showdetail-e.php?movieid=momo190323ca01a

Subsequent observations at this log were markedly different from those conducted before the cheating event. On 29 April, we did not observe any manakins, and on 5 May, we observed RB-BS and briefly saw two other adult-plumaged males that had previously been observed at the log, but no birds displayed. Not until 14 May 2017 did we again observe displays by six males, all of whom had been observed displaying prior to the attempted cheating event. The activity during the remaining three observations of the season were similar to those mid-May; although several males displayed, activity never returned to pre-cheating levels, and we never again observed a visiting female. This change did not reflect reproductive phenology elsewhere at the site; activity remained high at many of the other 30 logs in our study until at least the end of May.

Discussion

These observations provide a fascinating glimpse into the mechanisms that may constrain cheating in Pipridae and into the evolution of cooperative mating displays more generally. Although our observation is unreplicated, this lack of replication in fact highlights the incredible rarity of cheating (<0.0003 times per hour of direct observation, and 0.0000052 times per hour of video observation). Furthermore, the rarity of such events in the literature is notable given the tremendous amount of researcher effort dedicated to observing manakin leks over several decades. It is possible that because most direct observations are not also recorded on video or because confidence in the identity of individual birds can sometimes be low, some similar events may not have been reported by other researchers, thereby highlighting the benefits of video recording during observation of animal behavior.

The differences in male behavior before and after 23 April 2017 suggest that cheating can dramatically affect male behavior and interactions within social hierarchies and male–male alliances. Interestingly, cheating affected not only the two males and female directly involved, but seemed to erode the extended social hierarchy, at least temporarily. Additionally, because we subsequently observed no other female visits, it is possible that this event may have affected mating success of the dominant male.

We suggest that facultative male–male cooperation such as occurs in *C. altera* may be uncommon, in part because of elevated cheating risks to either the alpha male or the female, or both. In the event we witnessed, a non-dominant male clearly tried to cheat on the dominant male. If cheating destroys male–male alliances, then species that are obligate cooperators likely have too much at risk to cheat because solo displays result in low mating success. Alternatively, species with obligate solo male displays are always safe chasing away intruders, enabling them to tightly control the mating context. Facultative cooperation may thus be an adaptive valley between the peaks of obligate solo and cooperative systems. In the event we witnessed, it seems highly likely that the non-dominant male was also cheating the female given that (1) he oriented behind her prior to his approach and (2) she left the scene as soon as the non-dominant male attempted to mount her. When males cheat, females are robbed of mate choice; thus, females may magnify selection for either obligate solo or cooperative displays by preferring mating contexts in which they can be sure of the identity of the males from whom they accept sperm (McDonald 2010). If this is the case, the displays of *C. altera* represent a conundrum because the final stages of courtship take males out of sight of the female, and mating occurs immediately following behavior that likely affords little chance of individual recognition. Why sexual selection has resulted in display behaviors that appear to relinquish control of the mating context remains to be discovered.

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals and all applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflicts of interest regarding this work.

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