



Variation within and between courts in visual components of Swallow-tailed Manakin (*Chiroxiphia caudata*) display

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Abstract

Birds are well known for displaying courtship exhibitions shaped by sexual selection that involve combinations of visual, motor, and acoustic components. Among such multifaceted exhibitions are those of male piprids, which can perform coordinated or cooperative displays to attract females. Here we focus on the Swallow-tailed Manakin (*Chiroxiphia caudata*), endemic to the Atlantic Forest, whose displays include two or more males executing a cartwheel-type movement (“cooperative display”) and solo exhibitions. We used videography to describe and analyze male maneuvers and to test differences in display parameters between courts (where adult males perform coordinated/cooperative displays in groups of two to six individuals within an arena) and between dominant and subordinate males. We recorded displays of individuals from four courts in southern Brazil during two breeding seasons. We identified nine male display elements, five in cooperative, three in solo formations and one in other contexts, in addition to two elements performed exclusively by females. Sequences of male display elements were highly stereotyped, but three display parameters differed between courts: vertical flight height, distance from which males approached females and cartwheel velocity. Moreover, subordinates flew longer vertical flights than dominants. This variability suggests that females may evaluate courts based on display parameters, leading to their decision to remain at the perch, attend the solo display and eventually copulate. The vertical flight duration can also be a signal used during intrasexual communication, such as for hierarchy establishment. Our detailed description of male display attributes provides essential evidence that courts differ in motor parameters, and opens an avenue for further studies on sexual selection mechanisms in the Swallow-tailed Manakin and other manakins.

Keywords Atlantic forest · Lekking · Motor display · Pipridae · Sexual selection

Zusammenfassung

Variation visueller Komponenten der Schaubalz beim Blaubrústpipra (*Chiroxiphia caudata*) innerhalb und zwischen Balzarenen.

Vögel sind bekannt für ihr auffälliges, durch sexuelle Selektion geformtes Balzverhalten, welches Kombinationen aus visuellen, motorischen und akustischen Komponenten umfasst. Zu diesen facettenreichen Darbietungen gehören die der männlichen Schnurrvögel, welche zur Anlockung von Weibchen koordiniertes oder kooperatives Schaubalzverhalten ausführen können. Hier betrachten wir den für den Atlantischen Regenwald endemischen Blaubrústpipra (*Chiroxiphia caudata*), bei dem als Teil der Schaubalz zwei oder mehr Männchen einen radschlagähnlichen Bewegungsablauf („kooperative Schaubalz“) sowie Einzeldarbietungen zeigen. Mittels Videoaufnahmen beschrieben und analysierten wir die Manöver der Männchen und untersuchten diese auf Unterschiede bezüglich der Parameter des Balzverhaltens zwischen verschiedenen Balzarenen sowie zwischen dominanten und untergeordneten Männchen. Über zwei Brutsaisons hinweg nahmen wir Schaubalzen von Individuen aus vier Balzarenen in Südbrazilien auf. Wir identifizierten neun Schaubalzelemente bei den

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Männchen, fünf davon in kooperativen, drei in einzelnen Darbietungen sowie eine weitere in anderem Kontext auftretende; zusätzlich noch zwei Elemente, die ausschließlich von den Weibchen ausgeführt wurden. Die Abfolge der Schaubalzelemente war bei den Männchen hochgradig stereotyp, drei Parameter unterschieden sich jedoch zwischen den Balzarenen: vertikale Flughöhe, der Abstand, bis zu dem die Männchen sich den Weibchen näherten, und die Geschwindigkeit des Radschlags. Außerdem führten untergeordnete Vögel längere vertikale Flüge aus als dominante. Diese Variabilität legt nahe, dass die Weibchen die Arenen möglicherweise aufgrund der Darbietungsparameter bewerten, woraufhin sie entscheiden, ob sie auf der Sitzwarte bleiben, der Einzelvorstellung zuschauen und schließlich kopulieren. Die Dauer des Vertikalfluges kann auch ein Signal im Rahmen der intrasexuellen Kommunikation darstellen und zum Beispiel der Hierarchiefindung dienen. Unsere detaillierte Beschreibung der Attribute des männlichen Balzverhaltens liefert entscheidende Belege dafür, dass sich die Arenen hinsichtlich der motorischen Parameter unterscheiden und bereitet den Weg für weiterführende Untersuchungen zu den Mechanismen der sexuellen Selektion beim Blaubrústpipra und anderen Schnurrvögeln.

Introduction

Extravagant attributes in animals are unlikely to be favored by natural selection because they are costly or disadvantageous; nonetheless, they can determine the choice of sexual partners as they are often important quality signals (Andersson 1994). In general, larger or more ornamented individuals have advantages in mate competition since such attributes may reflect good health and resistance to disease (Møller and Birkhead 1994). Among sexual signals, behaviors that emphasize ornaments are widely distributed in several taxonomic groups. For instance, male dancing behavior has been recorded in Peacock Spiders (Girard et al. 2011), European Tree Frogs (Gomez et al. 2009), agamid lizards (LeBas and Marshall 2000), and birds of paradise (Scholes 2008), among others. These exhibitions reflect an individual's skill and vigor, and usually require intense physical activity, increased ability, persistence, and high-energy investment (Byers et al. 2010).

In birds, courtship presentations are mostly visual, with exhibitions of colored or specialized feathers in flight or in stereotyped body movements. Many birds also perform acoustic courtship displays and their vocal repertoire is usually important for female choice (Nowicki et al. 1998). Among the most interesting displays are those involving combinations of visual and sound stimuli, such as the leap display of the Blue-black Grassquit (*Volatinia jacarina*) (Manica et al. 2017) and the complex dance of Carotia's Parotia (*Parotia carolae*) (Scholes 2006). Exhibitions with multiple signals are also typical of manakins (Pipridae), in which courtship behaviors vary from simple (i.e., performed by a single male) to complex (i.e., performed synchronously and in a coordinated manner by several males) (e.g., Lill 1974; Foster 1977; Tello 2001; DuVal 2007a).

We studied the Swallow-tailed Manakin (*Chiroxiphia caudata*), a Pipridae species with a striking sexual dimorphism: adult males have blue body plumage, a red crown and black wings and neck, while females are completely

green (Sick 2001; Mallet-Rodrigues and Dutra 2012). Juveniles are similar to females in their early plumage stages, and acquire definitive plumage gradually over a 4-year-long process (Foster 1987; Mallet-Rodrigues and Dutra 2012). Adult males perform coordinated/cooperative displays in groups of two to six individuals in display perches within an arena (or court), usually defended by a dominant male (Foster 1981). Arena defense and attraction of females are performed by males across the breeding season by singing on a high and central perch in duets (Foster 1981) or choruses (Schaedler et al., 2019). After a female arrives at the display perch, the cooperative exhibition begins by two or more males producing repetitive and coordinated flight movements in sequence, directed towards the female, while simultaneously producing a *wah* vocalization (“cart-wheel type display”) (Foster 1981; Schaedler et al., 2019). A strident vocalization of the dominant male (*keekeekee*) (Schaedler et al., 2019), synchronized with hovering flight and strong wing beats, determines the end of the cooperative exhibition. In these courts, the dominant male may also display on his own to females (hereafter “solo display”), usually culminating in copulation (Foster 1981; Prum 1994). Despite male-coordinated displays being directed towards females, the audience can also be other males. While this is often suggested as being a practicing behavior or social interaction (DuVal 2007b; Lukianchuk and Doucet 2014a, b), the purpose of such behavior has yet to be studied in the Swallow-tailed Manakin.

The first, more thorough study of Swallow-tailed Manakins dates back to the 1980s (Foster 1981), and further information about this species has been limited to landscape ecology (Uezu et al. 2005; Boscolo and Metzger 2009), foraging (Hasui et al. 2009), relatedness and population diversity (Francisco et al. 2007, 2009). Knowledge about how sexual selection has driven the evolution of this species is scarce, and few studies have sought to understand this bird's social complexity (Foster 1981; Francisco et al. 2009; Brodt et al. 2013) and

breeding behavior (Zima et al. 2017), probably due to challenges related to tracking, marking and reencountering birds in the field. For instance, it is still unknown which display parameters are under female evaluation, and whether exhibitions vary among different groups of males; both of these are required conditions for promoting reproductive skew and strong sexual selection (Cotton et al. 2006). Thus, our aim in this study was to characterize the male Swallow-tailed Manakin display by describing the maneuvers (display elements) during cooperative and solo exhibitions. More specifically, we asked whether the motor display parameters of different courts, and of dominant versus subordinate males, differ.

Methods

Study area and period

We conducted this study during two periods, from September 2015 to February 2016 and from September 2016 to February 2017, which encompass the breeding season of the Swallow-tailed Manakin (Foster 1981; Zima et al. 2017). Our study site is an ~80-ha area located within Mananciais da Serra at Pico Marumbi State Park (48°59'W and 25°29'S), Piraquara, PR, Brazil, one of the largest Atlantic Forest remnants, comprising the Araucaria and Montane Atlantic Rainforests (Reginato and Goldenberg 2007).

Capture and marking

We searched for male courts throughout the study area and identified arenas by the acoustic detection of duets and choruses (Foster 1981; Schaedler et al., 2019). We identified primary (most active) and secondary (less active) display perches in each court by focal observations of display activities (see below).

Banding was carried out up to three times weekly using 6- to 12-m-long mist nets arranged ~15 m from the main court areas. We aged and sexed each captured individual following Mallet-Rodrigues and Dutra's (2012) classification and the following plumage stages: juvenile (completely dull-olive green plumage), formative (completely dull-olive green body feathers with reddish forehead and sometimes a blackish mask), pre-definitive (similar to formative, but blue and green feathers varying from a few to more abundant on the body), and definitive (complete adult plumage, with no green feathers). Females could be confused with males in their juvenile or formative plumage, therefore, we sorted adult females from male and female juveniles by the presence of an incubation patch and the absence of a labial commissure, red or

orange crown feathers or wing molt limit [i.e., evidence of juveniles' greater primary cover retention (Ryder and Durães 2005)]. We marked each individual with a unique sequence of three plastic colored bands for later visual identification, and a numbered metal band (CEMAVE/ICMBio).

Display behavior

We recorded cooperative and solo displays in four courts (C1–C4) using digital cameras (Sony models HDR-CX230, HDR-CX290, DCRSR47; and Casio EX-ZR850) placed at least 5 m from display perches for approximately 1–8 consecutive h (3.9 ± 1.8 h per court, total = 644.7 h), up to four times per week. We edited and analyzed videos using Windows Movie Maker (Microsoft 2012) to describe each of the stereotyped movements given below. To characterize all display elements, we only used recordings from displays attended by females and in which they were visible for at least 10 s on the perch.

To characterize the repertoire of maneuvers, we described and named each element by partitioning the entire sequence into independent, unique and stereotyped movements, executed similarly by different individuals. Element names followed the literature whenever the Swallow-tailed Manakin movements were similar to those executed by other manakins [e.g., *Chiroxiphia paraola* (Snow 1963), *Chiroxiphia caudata* (Foster 1981), *Chiroxiphia lanceolata* (DuVal 2007a) and *Chiroxiphia linearis* (Lukianchuk and Doucet 2014a)].

To compare the cartwheel display between courts and between males of different status, we measured display parameters, which included those of maneuvers that likely indicate male skill and vigor (Byers et al. 2010; Barske et al. 2011; Fusani and Schlinger 2012; Manica et al. 2017). We extracted still images from the videos to measure the following motor parameters in ImageJ (Rueden et al. 2017): (1) vertical flight height (the distance between the perch and the male's beak, when the male's body was positioned at a 90° angle, at the highest point of vertical flight); (2) vertical flight duration (the time the male took to reach his maximum flight height), (3) distance to female (distance between the horizontal projection of the male's beak when he is at maximum flight height and the center of the female's body); (4) cartwheel velocity (ratio between the distance flown by males from takeoff to landing and flight duration) (Fig. 1). We used a measuring tape to measure each perch diameter, which was then used as a scale to convert all measurements made from the still images. We measured all four display parameters at the beginning, middle and end of three different cartwheel displays in each court, sampled on different days, whenever possible.



Fig. 1 Example of a video still showing methods for calculating male motor display parameters: vertical flight height (*a*), vertical flight duration (*b*), distance to female (*c*) and cartwheel velocity (*d*). See text for details of protocols for measurement procedures

Statistical analyses

We analyzed the sequence of cooperative and solo display elements using first-order Markov chains to build transition probability matrices that demonstrate the likelihood that a given display element would be preceded by another. To calculate probabilities, we determined the frequency of exhibition of each element, and identified which element was produced in what sequence, i.e., within <30-s intervals. We divided the number of exhibitions of each element by the total number of elements produced in the same sequence. We used the same procedure to calculate the probability of solo displays occurring after a cooperative display, considering that they were produced in sequence if separated by an interval shorter than 1 h. In this analysis, we only considered displays performed in the presence of a female, therefore one element (tail vibration) (see “Results”) was not included. We built transition probability matrices separately for cooperative and solo displays.

We tested for the relationship between display parameters—vertical flight height, vertical flight duration, distance to female, and cartwheel velocity—using linear mixed models (LMM) for each pair of variables and considered male identity as a random effect term. We compared each of these four motor parameters between display courts and between males of different status (dominant and subordinate) using one LMM for each parameter, also considering male identity as a random effect term. We performed a post hoc Tukey test with

Bonferroni correction to compare significant parameters between each pair of display courts.

We used the Shapiro–Wilk’s test to assess whether variables had a normal distribution; we log-transformed vertical flight height and duration, and square-root-transformed distance to female. We validated models by plotting residuals by fitted values to check for homoscedasticity and by using Shapiro Wilk test to check for residual’s normality. We built all LMM using the lme4 package (Bates et al. 2015) and made post hoc pairwise comparisons using the mult-comp package (Hothorn et al. 2008) in R 3.2.1 (R Core Team 2015). In all tests, we adopted a significance value of 0.05. We present all values as mean \pm SD, except when mentioned otherwise.

Results

Two out of the four studied courts had more than one display perch, totaling 11 monitored perches (Table 1). We captured and banded 95 individuals, 73 of which were males (17 with definitive plumage, 29 with pre-definitive plumage and 27 with formative plumage) and ten adult females. Twelve individuals could not be sexed because they had either juvenile (seven individuals) or formative plumage (five individuals). We registered 30 banded males (41% of the captured males) performing display activities at the monitored perches. The number of males in cooperative displays ranged from two

Table 1 Summary of data recorded in each Swallow-tailed Manakin display court

Parameter	C1	C2	C3	C4	Mean SD
Display perches	4	1	5	1	2.70 ± 2.10
Males in cooperative displays (minimum–maximum)	2–4	3–4	2–3	4–5	2.52 ± 0.93
Cooperative displays with female attending/bout	0.27 (8)	0.63 (6)	0.14 (10)	0.15 (3)	0.81 ± 0.30
Cooperative displays without female attending/bout	0.91 (27)	0.94 (9)	0.36 (25)	1.02 (21)	0.30 ± 0.23
Solo display/bout	0.64 (19)	0.73 (7)	0.29 (20)	0	0.42 ± 0.34
Copulations/bout	0.41 (12)	0.52 (5)	0.23 (16)	0	0.29 ± 0.23

Rates are presented per sampling bout (5 h) with the total number of displays in parentheses

to five (Table 1; Online Resource 1), all of which exhibited pre-definitive or definitive plumage. Females attended cooperative and solo displays more often at courts C1 and C2, while cooperative displays without females in attendance occurred at similar rates across all courts with the exception of C3 (Table 1). We registered copulations in C1, C2 and C3, but they were more frequent in C1 and C2 (Table 1).

Characterization and sequence of display elements

We recorded 355 exhibitions of 11 elements (Table 2). Males performed five elements in cooperative displays and three in solo displays (Table 2; Fig. 2; Online Resource 1). Dominant males were the only ones to produce two elements of the cooperative displays and all elements of

Table 2 Descriptions of male and female Swallow-tailed Manakin display elements and their respective duration (in seconds)

Element	Description	Sex	Duration mean ± SD (range) ^a	<i>n</i>
Cooperative display				
Cartwheel flight	Sequential and repeated hovering flight towards the female in a movement that resembles a circle (or wheel)	Male	103.5 ± 97.7 ^b (12–401)	53
<i>Keekkeke</i> ^d	Strong wing beats and a strident onomatopoeic vocalization	Male	2.1 ± 0.8 (1–3)	30
Tucked wing-flick ^d	Fast wing flaps while perched	Male	8.5 ± 2.5 (3–13)	27
Bow ^e	Subordination position, with males lowering their heads and raising their tails while perched	Male	11.4 ± 2.8 (7–20)	29
Bill wipe	Scratches branch with the bill	Male	7.5 ± 13.2 (1–66)	41
Solo display				
Head-up-and-down ^d	Up-and-down head movements	Male	6.2 ± 13.5 (1–110)	65
Butterfly flight ^d	Short-distance slow flights between perches	Male	– ^c	– ^c
Bow before copulation ^d	Subordination position, with the dominant male lowering his head and raising his tail next to the female	Male	1.0 ± 0.2 (1–2)	41
Other contexts				
Tail vibration	Tail feather and sideways movements, lightly beating wings	Male	19.4 ± 25.8 (1–85)	16
Back-and-forth	Wing vibrations and lateral movements	Female	56.7 ± 60.2 (2–233)	53
Loop	Fast sideways jump	Female	0.33 ± 0.02 (0.33–0.36)	3

^aThe duration of cooperative and solo elements was extracted only from female-attended displays

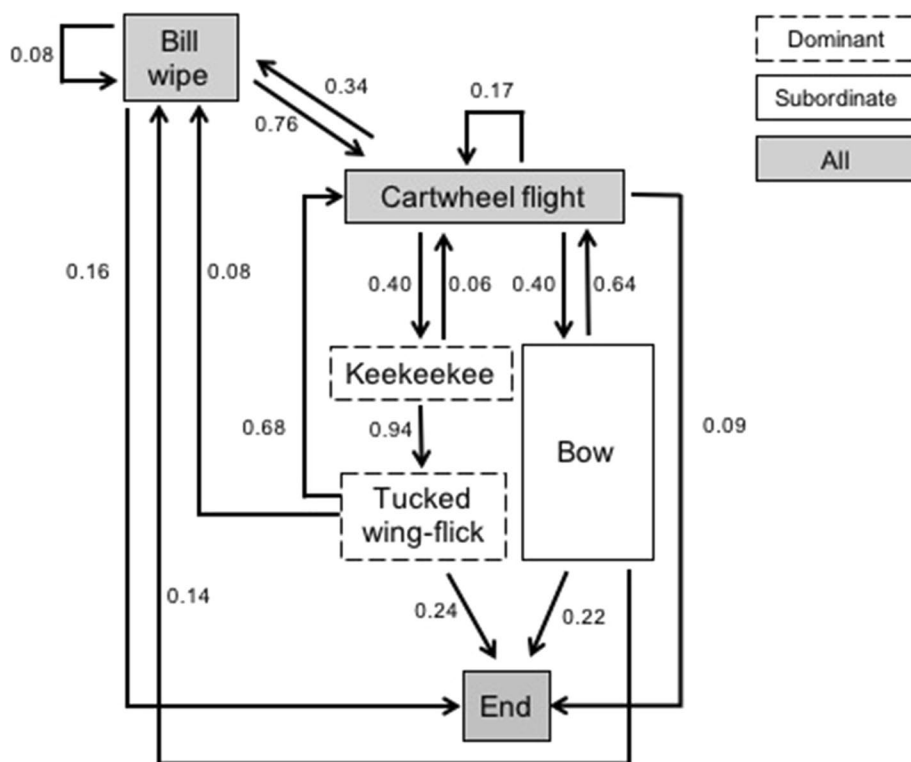
^bOnly elements > 10 s

^cButterfly flight duration was not evaluated because it included movements that demanded extrapolation of the limits of the camera view angle

^dElements produced only by dominants

^eElements produced only by subordinates

Fig. 2 Sequence of cooperative display elements in exhibitions of male Swallow-tailed Manakins. Arrows indicate transitions between elements ($n=229$), boxes indicate individuals that performed the element (white boxes with dashed outline dominants only, white boxes with continuous outline subordinates only, shaded boxes all individuals), numbers indicate the probabilities of each transition



the solo displays (Table 2), as well as copulations ($n=37$), all of them occurring after the solo display. Elements of the display may be very brief or may be performed for longer periods (1–401 s; Table 2). The cooperative display starts when two or more males arrive at the display perch, perform “bill wipes,” characterized by quick scratches with the bill on the branch, and initiate “cartwheel flight” (Fig. 2). Cartwheel flight, as described by Foster (1981) and Sick (2001), is composed by a sequence of repeated flights made by all males, departing from the perch where they are positioned in a row. The male at the front of the row performs hovering flight directed towards the female, tilts his head downwards and then returns to the perch, usually at the last position in the row. The complete movement resembles a circle (or wheel), and the bird accelerates as it advances towards the last circling flight (Foster 1981). Sometimes the number of males during the cartwheel flight varies, with new males joining the group and/or participating males leaving the dance. By the end of the cartwheel flight phase, dominant and subordinate males engage in different elements of the display (Fig. 2): the dominant male produces the *keek*, a combination of strong wing beats and a strident onomatopoeic vocalization (Schaedler et al., 2019), and follows this with the “tucked-wing flick,” characterized by fast wing flaps while the bird is perched on a nearby branch with its back to the female (white boxes with dashed outline, Fig. 2). Subordinates synchronously adopt a “bow” position, lowering

their heads, raising the tail while perched, and keeping themselves in this position for a few seconds (white boxes with continuous outline, Fig. 2). The dominant and subordinates may follow this with the bill wipe element, start the cartwheel flight over again or end the exhibition (shaded boxes in Fig. 2).

Solo elements were produced following the cooperative display in 24% of the records. During this display, the dominant male performs a variable combination of three sequential elements (Table 2, Fig. 3, Online Resource 1): “head-up-and-down,” in which the male makes fast head movements while facing the female; the “butterfly flight,” short-distance slow flights between the display perch and nearby twigs; and “bow before copulation,” a similar posture to the bow display of subordinates, but in this case preceding copulation. Another element was also recorded as unrelated to the cooperative and solo displays—the “tail vibration”—which includes tail feather movements while individuals move sideways and lightly beat their wings (Online Resource 1). Tail vibrations were never produced when there was a female in attendance at the arena and were only recorded 16 times. Remarkably, we also recorded two female display movements directed towards males (Table 2; Online Resource 1): the “back-and-forth,” which included wing vibrations and lateral movements on the display perch while watching the dominant male performing the solo display; and a “loop,” similar to a sideways jump while males were vocalizing around the perch after a cooperative display event.

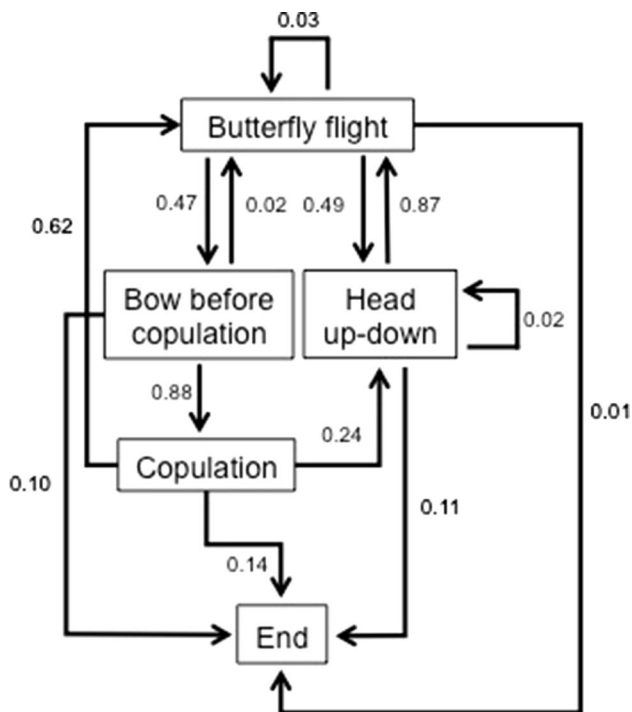


Fig. 3 Sequence of the solo display elements in exhibitions of dominant Swallow-tailed Manakin males. Arrows indicate transitions between elements ($n=221$) and numbers indicate the probabilities of each transition

Displaying females were only seen twice in our recordings, therefore we consider their recorded behaviors rare.

Differences among display courts and social status

To obtain and compare motor parameters (vertical flight height, vertical flight duration, distance to female and cartwheel velocity) among courts, we used data from all four courts (C1–C4). On average, males performed cooperative exhibitions flying at heights of 14.0 ± 3.5 cm, ascending in 0.12 ± 0.03 s, approaching the female at distances of 6.4 ± 3.6 cm, and at a velocity of 17.7 ± 6.2 cm s⁻¹ during the cartwheel display. Vertical flight height increased with distance to female ($\beta \pm \text{SE} = 0.37 \pm 0.09$, $p < 0.01$) and cartwheel velocity with vertical flight height ($\beta \pm \text{SE} = 0.38 \pm 0.06$, $p < 0.01$), but no other pair of motor parameters was related to each other ($\beta \pm \text{SE}$: height versus duration, 0.02 ± 0.07 ; duration versus velocity, -0.17 ± 0.09 ; distance to female versus duration, 0.08 ± 0.07 ; distance to female versus velocity, 0.05 ± 0.07 , all $p > 0.05$). Comparisons of between-court parameters revealed differences in flight height, distance to female and cartwheel velocity, but not in vertical flight duration (Table 3). Males in C2 showed the lowest vertical flight height and cartwheel velocity and males in C3 displayed farthest from females (Fig. 4). Males in C1 and C3 achieved

the fastest cartwheel velocity and males in C3 and C4 performed the highest flights (Fig. 4). We found that dominant and subordinate males differed only in vertical flight duration, with subordinate males taking longer to perform their flight compared with dominant males (Table 3).

Discussion

Our study is the first to describe maneuvers in displays of the Swallow-tailed Manakin. We found that two to five males may engage in cooperative display and that 11 elements comprise the display repertoire of males (nine elements) and females (two elements). Transitions between elements were stereotyped, but we also found significant differences between maneuvers of males from four courts. Using videography data we found differences when comparing parameters of flight height, distance from which males approached females, and cartwheel velocity. Furthermore, when comparing males of different social status, we found that subordinates flew longer vertical (ascending) flights than dominants.

Differences between courts in motor parameters are indicative of different display qualities, which, if perceived by females, could affect their decision to attend solo displays. Males that succeed in keeping females in the court to watch their solo displays will benefit because solo displays always preceded copulation. Our results for the Swallow-tailed Manakin indicate the existence of an important prerequisite for the operation of sexual selection in the study population, i.e., the existence of variability across individuals or groups of individuals in display ability (Darwin 1871). Males performing displays indicating superior genetic quality or attractiveness (Byers et al. 2010; Barske et al. 2011; Prum 1997, 1998), such as those able to combine higher flights, higher velocities and closer approaches to females (e.g., C3 in Fig. 4), should be preferred. Another outstanding feature in the Swallow-tailed Manakin display is that cooperative displays are apparently variable depending on the number of individuals participating and the number of interruptions due to newcomers during the cartwheel display. While many studies have shown that display attributes are indeed related to differential breeding success of males (e.g., Fusani et al. 2007; Byers et al. 2010; Barske et al. 2011; Manica et al. 2016), this remains an open question for Swallow-tailed Manakins and will only be answered in the future with larger samples of recorded copulations in several different courts and populations. Although we did not test the female preference hypothesis, our study raises important questions about the operation of sexual selection in this species: how many males are needed for females to attend the display, do females prefer larger groups of displaying

Table 3 Results of linear mixed models evaluating the relationship of the motor display parameters (vertical flight height, vertical flight duration, distance to female and cartwheel velocity) with court identity and male status (dominant and subordinate)

Response variable	Predictor	Estimate (SE)	X^2	df	p -value
Vertical flight height ($n = 120$)	Intercept	− 0.59 (0.32)	51.29	3	< 0.001
	Court ^a				
	C2	− 1.09 (0.31)			
	C3	1.07 (0.32)			
	C4	0.85 (0.36)			
	Status ^b		3.03	1	0.082
Subordinate	0.50 (0.28)				
Vertical flight duration ($n = 120$)	Intercept	− 0.65 (0.39)	0.88	3	0.831
	Court ^a				
	C2	0.23 (0.40)			
	C3	− 0.15 (0.41)			
	C4	0.13 (0.45)			
	Status ^b		5.01	1	0.025
Subordinate	0.80 (0.36)				
Distance to female ($n = 120$)	Intercept	− 0.91 (0.26)	59.96	3	< 0.001
	Court ^a				
	C2	0.86 (0.27)			
	C3	2.05 (0.27)			
	C4	0.34 (0.29)			
	Status ^b		2.17	1	0.089
Subordinate	0.35 (0.24)				
Cartwheel velocity ($n = 120$)	Intercept	0.54 (0.21)	46.73	3	< 0.001
	Court ^a				
	C2	− 1.62 (0.24)			
	C3	− 0.36 (0.23)			
	C4	− 0.79 (0.24)			
	Status ^b		0.0001	1	0.992
Subordinate	− 0.002 (0.20)				

Male identity was considered a random effect term

p -values < 0.05 are in *italic*

^aC1, C2, C3 and C4, with C1 as the reference level

^bDominant (reference level) or subordinate

males, or are displays of larger groups less organized and less preferred by females?

In contrast to the other parameters of the motor display, vertical flight duration was invariable between courts, but was higher for subordinates when compared to dominants. These results suggest that males could use this parameter as an intrasexual signal among individuals of the same court, necessary for hierarchy establishment, although other parameters may also be involved in these contexts [e.g., age or aggression levels in other *Chiroxiphia* (DuVal 2007b; Lukianchuk and Doucet 2014b)]. Also, other elements were performed only during male–male interactions, such as the bill wipe and tail vibration, indicating that these movements do not comprise the court exhibition repertoire directed towards females, as suggested for *C. linearis* (Lukianchuk and Doucet 2014a). Alternatively,

differences between dominant and subordinate males could signal their status, thus influencing female choice and hence leading to increased copulation success for dominant males. Future studies with genetic parentage data should provide evidence for female sexual choice, since copulations were recorded only for dominants.

We recorded one unique element of the Swallow-tailed Manakin display, in comparison to that of congeners—the head-up-and-down—a component of the solo display. Also unique to this species was the female loop, a very rapid movement that could have been easily missed without videography analyses. Despite these exclusive movements, the motor display repertoire of the Swallow-tailed Manakin largely resembles those recorded for other *Chiroxiphia* [11 elements in *Chiroxiphia lanceolata* (DuVal 2007a); 16 in *Chiroxiphia linearis* (Lukianchuk and Doucet 2014a), nine

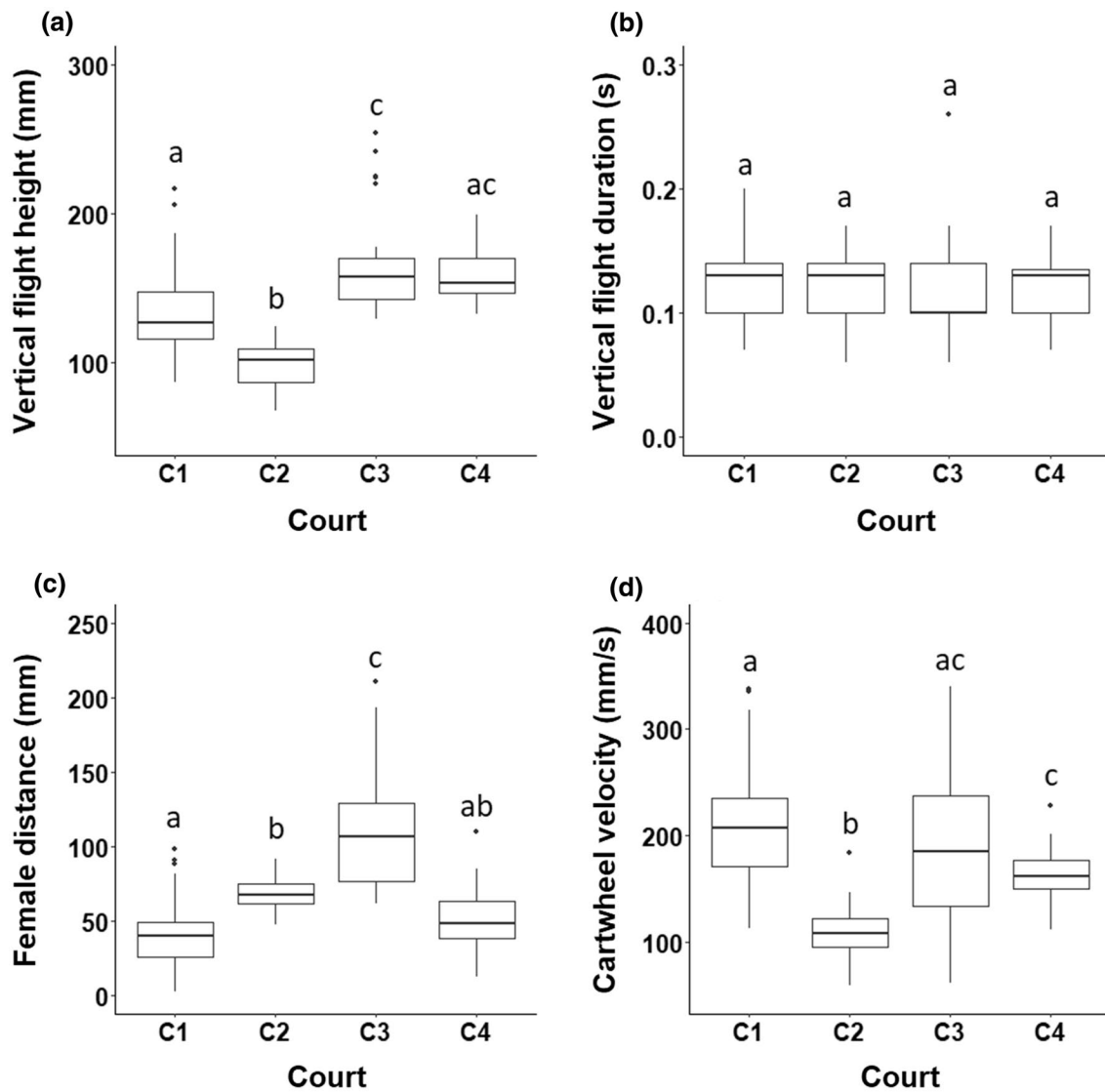


Fig. 4 Boxplots showing differences between courts in male Swallow-tailed Manakin motor parameters: **a** vertical flight height, **b** vertical flight duration, **c** female distance and **d** cartwheel velocity. All

motor parameters differed among courts, except for vertical flight duration. Letters above each box indicate statistical differences after post hoc comparisons

in *Chiroxiphia pareola napensis* (Cárdenas-Posada et al. 2018)]. Highly similar elements include the male's cartwheel flight, *kekekeke*, tucked wing-flick, bow, bow before copulation, butterfly and bill wipe and female's back-and-forth during the male solo display, described here for the first time. Foster (1981) had already mentioned female excitement during the display, but we did not register the female "hopping-up-and-down" during the cooperative display, an element previously described. We recorded the visible responsiveness of females to the males' cooperative dance, seen by their quick and slight head movements accompanying male flights, and during the solo display, more specifically while the dominant male performed the butterfly flight. We suggest female attentiveness to male display can be a

good predictor of their interest in males for copulation, as shown in other Pipridae (DuVal 2007a) or Ptilonorhynchidae (Patricelli et al. 2002), and should be considered in future studies about female choice in this species.

The newly described display elements of the Swallow-tailed Manakin, such as the tail vibration and bill wipe, were only possible due to the use of videography, including a few events using high-speed recordings. Our low sample size for the tail vibration is probably a detection failure while shooting at the standard 30 frames per second (f.p.s.), a default recording setting of most video cameras. Similarly, *kekekeke* is hardly captured if filming is not carried out at > 120 f.p.s. Video recordings have unveiled a wealth of display repertoires in several bird species (e.g., Ota et al. 2015;

Scholes et al. 2017; Manica et al. 2017), including other Pipridae such as *Manacus manacus* (Fusani et al. 2007), *Machaeropterus deliciosus* (Bostwick and Prum 2005), *Manacus vitellinus* (Barske et al. 2011; Bodony et al. 2016) and *Xenopipo atronitens* (personal communication in Lindsay et al. 2015). We expect that future studies using such techniques will provide even more mechanistic details about display maneuvers and sound production in Swallow-tailed Manakins, such as precise synchronization of wing beats and beak movements during the cartwheel and during the *keekeeke* vocalization.

Our descriptions of all display elements allowed us to detect a striking stereotyped pattern in the cooperative and solo displays. The transitions between elements were highly predictable, similarly to other *Chiroxiphia* (DuVal 2007a; Lukianchuk and Doucet 2014a). In the Swallow-tailed Manakin the sequential and multiple repetitions of the cartwheel flight, *keekeeke*, tucked wing-flick and bow elements comprise the most striking and typical dance of this species. Nonetheless, one of the most stereotyped transitions was between solo display elements (butterfly flight, followed by head-up-and-down, butterfly flight again and bow before copulation) which, ultimately, results in copulation. Sexual selection may have favored such predictability to provide honest information to receivers (Zahavi 1980), which may have shaped the evolution of display behavior. A consistent and stereotyped pattern could reflect improved male ability in exhibitions and, consequently, may be favored by females. This hypothesis is supported by an experiment in which a structural manipulation of the display area of *M. vitellinus* led to an imperfection in the final pre-copulatory display performance, which consequently lowered copulation chances (Coccon et al. 2012). Also, in Lance-tailed Manakins, displays for females were more predictable and coordinated than displays in the absence of females (Vanderbilt et al. 2015). In addition to the consistency of the displays, we also emphasize that displays can be energetically costly because they are often produced uninterruptedly during long bouts. For example, our longest record of the cartwheel element was 6.7 min long (Table 1). We suggest that if females care about consistency and costly displays, they should greatly focus both on the transitions of elements and also on display intensity, both of which may reliably indicate the quality of the potential sexual partner.

In animals, male displays are generally of paramount importance in achieving copulation (Andersson 1994; Byers et al. 2010), so it is crucial that we understand the mechanisms of visual cues and their influence on female choice. Our study is the first to detail the display of the Swallow-tailed Manakin, a species for which such information was lacking, which left us with a large gap in our understanding about the genus and the family (e.g., Prum 1998; Lindsay et al. 2015; Marques Silva et al. 2018), despite being one of

the most easily captured birds in the Atlantic Forest (Rodrigues et al., unpublished data), and exhibiting one of the most complex, fascinating sexual and social systems in this clade. We further highlight the importance of documenting and understanding the breeding behavior of this species in light of the fact that it inhabits remnants of the Atlantic Forest, a highly endangered biome that has been reduced to only 6.7% of its original range (Loiselle et al. 2010). Here we provide a detailed description of the motor traits of this species' display, which shows high variability between different courts and according to male status (i.e., dominant or subordinate). In addition to traits indicating attractiveness and individual quality, such as consistency of the dance (Vanderbilt et al. 2015) and plumage color (Keyser and Hill 2010), we suggest that Swallow-tailed Manakin females can evaluate the motor parameters we measured here when choosing to attend a specific perch. This result should be taken into consideration in future studies that attempt to understand how sexual selection acts upon this species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in the studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (license nos.: Sistema de Autorização e Informação em Biodiversidade no. 44439, Centro Nacional de Pesquisa e Conservação de Aves Silvestres no. 1195110 and Ethics Committee of the Universidade Federal do Paraná no. 820).

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