

High-Speed Video Analysis Reveals Individual Variability in the Courtship Displays of Male Golden-Collared Manakins

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Abstract

The males of the Golden-collared manakin (*Manacus vitellinus*), a passerine bird of the Neotropical region, perform elaborate courtship displays that are among the most spectacular in the animal kingdom. During a 7-mo long breeding season, male manakins aggregate in leks of up to 12 individuals, and each male clears a small 'court' on the forest floor where he spends several hours per day performing his displays either with or without the presence of a female. Like males of other manakin species, males of *M. vitellinus* produce loud mechanical sounds with their wings during the displays. The elaborate displays of the manakins are thought to be the result of sexual selection, which is particularly intense in lekking species in which females choose their mate mainly on the basis of behavioural and morphological features. However, we know little about differences in display between male manakins which may be related to individual differences in reproductive success. A quantitative, detailed analysis of the courtship displays has been difficult because the birds' movements are too fast to be studied with standard video recording techniques. For the first time, we recorded the displays of male Golden-collared manakins in the forest of Panama with a high-speed camera that allows a time resolution 5–40 times higher than that of a standard video camera. We found that several elements of the displays differed significantly between individuals. In addition, the slow-motion analysis revealed the features of the displays that had not been described in previous studies. Individually different features of the displays may form the basis for female choice and will allow testing hypotheses about the evolution of the manakin displays by sexual selection and their importance for speciation mechanisms in the genus *Manacus*.

Introduction

In several taxa, males perform elaborate courtship displays during the reproductive season. In some cases, courtship displays are performed by both sexes and might function to co-ordinate reproductive physiology and maintain pair bonds (Lehrman et al. 1961; Tinbergen 1965). However, the major force

behind the evolution of sexually dimorphic courtship displays is sexual selection. This is particularly obvious in species where the male carries bright or bulky ornaments that may increase predation or increase energy consumptions and thus reduce survival (reviewed by Andersson 1994; Darwin 1871; Zahavi 1975). Behaviourally complex courtship displays face similar costs (but see Borgia 1993;

Gustafsson & Sutherland 1988). Among birds, manakins of the tropical family Pipridae perform some of the most spectacular, complex and acrobatic displays. In the bearded manakins (*Manacus* spp.), males clear a display arena or court between small vertical saplings on the floor of secondary forest. Over the course of their long-breeding season, males spend most of the day in and around the arena performing a variety of courtship displays that include production of mechanical sounds with their wings (wing-snaps) (Chapman 1935; Lill 1974; Snow 1962). In this genus, several traits seem to undergo sexual selection: males are brightly coloured, and choose the location of the arena and modify the settings of their displays to enhance contrast and thus visibility (Uy & Endler 2004). Therefore, in *Manacus*, the courtship displays involve morphological, landscaping, site choice and behavioural specializations, with a complexity of traits which resembles that found in bowerbirds (Patricelli et al. 2003). The importance of displays for male manakins is highlighted by their lek mating system. Female manakins obtain nothing else than sperm by their mates, and thus presumably base their choice only on the complex features of the display. In *Manacus* leks, few males monopolize most of the matings (Lill 1974; Shorey 2002; Stein & Uy 2006), and asymmetries in reproductive success between males lead to increased sexual selection (Andersson 1994).

Manakin displays have long attracted the curiosity of researchers; however, we still do not know how different aspects of the displays are used by females to choose males. The size and the condition of the male and the centrality of the court in the lek are correlated with mating success in *M. manacus* (Shorey 2002). Recent work has shown that the bright plumage of the collar and the level of contrast with the background resulting from court clearing are correlated with mating success in *Manacus vitellinus* (Uy & Endler 2004) (Stein & Uy 2006). The complexity and the high levels of specialization of the behavioural patterns, however, strongly suggest that these components of the display are subject to sexual selection as well (Prum 1998). In fact, phylogenetic analyses indicate that behavioural components of displays evolved before the morphological traits featured in the same displays (Prum 1990).

To understand how sexual selection operates on manakin displays, it is necessary to know which aspects and structural features of the display vary between individuals and thus constitute a base for selection. A major factor hindering the study of manakin displays is the speed of the bird

movements. In fact, the birds move so fast that it is not possible to study their displays in details using the standard techniques. Recently, portable high-speed video cameras have become available which allow recording up to 1000 frames per second (fps) compared to the standard 25–30 fps of user camcorders. Such cameras have been recently used to study the mechanical sound production in several manakin species (Bostwick & Prum 2005) (Bostwick & Prum 2003).

In this work, we have used high-speed video recording to study the courtship displays of the Golden-collared manakin (*M. vitellinus*) in the forests of Panama. The recordings were first used to describe the details of the behavioural displays. Then, we selected a series of variables that, in our opinion, could be good candidates to represent the male quality. These variables were measured in a sample of courtship displays from several males and then analysed for individual differences. Our aim was to identify individually different features of the display which can be related to condition, energy expenditure, sensorimotor co-ordination, and thus could be indicators of male quality.

Methods

Field Sites and Dates

The study was conducted in areas of secondary forest around Gamboa (9°07'N, 79°42'W), Province of Panamá, Republic of Panama, where we have been studying Golden-collared manakins since 1995. Eleven males from three different leks were caught with mist-nets and marked with colour leg bands for individual recognition. Video recordings (see below) were conducted between Mar. and Apr. All procedures were authorized by the Smithsonian Tropical Research Institute, the Autoridad Nacional del Ambiente of Republic of Panama and the UCLA Chancellors Animal Research Committee.

Video Recordings

The displays of the birds were recorded with a high-speed camera (MotionMeter, RedLake Inc., San Diego, CA, USA) at 125, 250 or 500 fps. The camera was mounted on a tripod and positioned at 4–5 m from the centre of a male's court. Recording was remotely controlled by the observer who was sitting in a hide about 10–12 m from the arena. Within 2–5 d, the focal bird habituated to the presence of the camera and observer. In the following days, during

two recording sessions (06:30–09:30 and 12:30–16:00), we recorded a series of display sequences. Because the observer had to reach the camera to download the high-speed videos to a camcorder, we could acquire only one sequence for each courtship bout. Thus, repeated courtship sequences from one individual were usually collected within 1–2 d, in the range of 06:30–16:00. During this time, there are large changes in environmental parameters including humidity, temperature and light intensity. In addition, the activity of neighbouring males and the number of females visiting the lek change considerably during the day, influencing the motivation of birds to display. Therefore, replicate sequences for each male were collected in different environmental and social conditions. Several factors such as the cost of the equipment, the time required by birds to habituate to the camera and the relative short duration of the dry season hindered our capacity of repeating recordings sessions for each male across one breeding season.

About 30% of the recordings were not of the quality required for the quantitative analysis, mainly because the frames were under- or overexposed. We collected a total of 60 workable display sequences from 11 banded males. Depending on the recording rate, sequences of 16 s (at 125 fps), 8 s (at 250 fps), or 4 s (at 500 fps) were recorded, slowed-down at 25 fps and transferred to Digital Videotapes by means of a camcorder (Sony) for later analysis. We also measured the distance between the vertical

saplings delimiting the court that had been used by birds during their displays (see below).

Behavioural Analysis

The videotapes were transferred to a PC and formatted to make them suitable for further analysis. All behavioural analyses were performed with The Observer Video Pro 4.0 (Noldus Information Technology, Wageningen, The Netherlands). The following description of the courtship display is based on our observations that were compared with those of previous studies on *M. vitellinus* (Chapman 1935; Day et al. 2006; Fusani et al. 2007; Schlinger et al. 2001) and on other *Manacus* species (Bostwick & Prum 2003; Lill 1974; Snow 1962).

The most conspicuous display performed by the male Golden-collared manakin in its court is the snap-jump display (Fig. 1). This display is actually the assemblage of several behavioural patterns and mechanical sounds that to a certain extent can also be observed in other behavioural contexts. The snap-jump display is always performed in the bird's court, although it can be observed sometimes in other locations in a simplified form. The court usually has an elliptical shape and is delimited by vertical saplings. Courts are prepared at the beginning of the breeding season and cleared daily of leaves and small branches. Males perform the snap-jump displays several times a day. From their favourite perch, usually a horizontal branch 2–5 m above the court, usually a horizontal branch 2–5 m above the court,

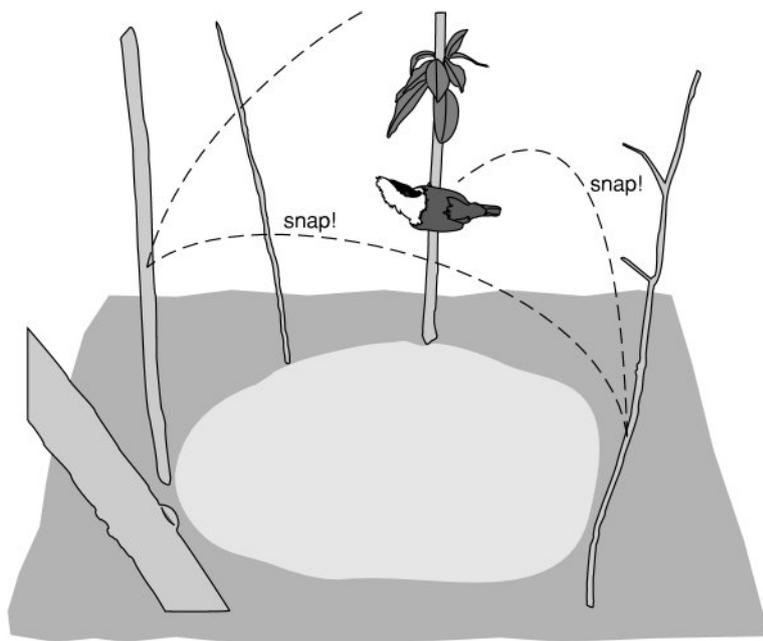


Fig. 1: A schematic representation of the snap-jump display of a Golden-collared manakin. The bird comes down from a perch 2–5 m above the court and lands on one of the vertical saplings delimiting the court. Then, he jumps towards another sapling and produces a loud snap in midair by a very fast upward movement of the wings that come in contact above the back of the bird. The snap-jump can be repeated up to 20 times in a row.

the male descends to the court with a vertical zigzag and lands on one of the saplings that delimit the court. From there, he jumps towards another sapling and produces a loud snap in midair. The number of jumps (and snaps) that form a display goes from a minimum of 1 to a maximum of 20. The courtship routine often ends with a spectacular variant of the snap-jump display, the 'grunt-jump'. The male lands on one particular sapling called the 'mating sapling' and then jumps making a wingsnap, lands on the ground and then jumps back to the mating sapling producing a 'grunt' sound. Females observe the display from perches above the court. If they find the male particularly attractive, they might then decide to enter a male's court and observe his display more closely by following him in the jumps. This first level of selection (courtship success) is highly correlated with the mating success (Stein & Uy 2006). If a female accepts to mate, she will perch on the mating sapling, while the male slides down the sapling to literally land on the top of the female perched below him.

After having screened all the videotapes and described in details the snap-jump display (see Results), we selected a number of behavioural variables to be analysed. We selected features of the snap-jump display which were shared by most individuals, could be measured with accuracy, were unambiguous, and might represent the condition, resistance, and motor co-ordination of the birds and be, therefore, good candidate indicators of male quality.

The selected variables were: *on perch*: amount of time spent perching on a sapling between two jumps; *jump duration*: duration of the jump; *beard up*: time required for the bird to resume his statuary posture with the erected beard at the end of the jump, from the moment of landing to the freezing of the posture; *jump speed*: duration of the jump/distance between the two saplings (we selected the jumps made between the two most used saplings) *snap frequency*: the number of wingsnaps per second during a snap-jump display.

For all variables, we calculated a sequence mean, i.e. the mean for all occurrences of a variable within a recorded display sequence. These values were then used for the statistical analysis of individual differences, comparing therefore the variance within individuals with the variance between individuals. Inter-individual differences for behavioural variables were analysed using the Kruskal–Wallis non-parametric ANOVA. All statistical tests were two-tailed and the significance level was set at $\alpha = 0.05$.

We recorded only four sequences in which a female-plumaged bird joined the court owner during the display, in three different courts. These events are relatively rare and only few males are able to attract females inside their court. These sequences were used for the behavioural description but were not included in the quantitative analysis of individual differences, and are reported separately.

Results

Description of Courtship Behaviour

We start this section with a description of aspects of the courtship displays that have not been described in previous reports and were revealed by the analysis of sequences recorded in the field with a high-speed camera.

During the snap-jump display, males perform on average 0.66 ± 0.05 snaps/s (*Snap frequency*, Table 1). The speed of the birds during a jump (*Jump speed*) is 2.85 ± 0.13 m/s, and jumps have an average duration (*Jump duration*) of 266 ± 6 ms. Between each jump, males spend 948 ± 91 ms resting on the sapling (*on perch*). A feature of the display highlighted by the slow-motion analysis is the fine control of the posture. Just before landing, the bird opens the wings to turn in midair and lands with his head pointing towards the centre of the court. After landing, the bird reassumes rapidly (*Beard up* = 53 ± 1 ms) his rigid, statuary posture that characterizes the display as much as the movements. The 'beard', i.e. a group of long, erectile feathers that are located at the base of the lower beak, is pointed to the centre of the court, and the posture is rigidly maintained until the next jump.

Also in the case of the grunt-jump, the high-speed analysis revealed the precise structure of the display. When the male lands on the mating sapling, he turns his body so that his back is directed towards the ground. Then, he jumps and makes a wingsnap while doing a cartwheel or a back-flip and lands on the ground with the wings partially open. After a brief pause, he takes off with a rapid vertical flight flapping the wings very fast, which produces the typical grunt sound (Fig. 2; Supplementary Video 1).

The whole courtship sequence resembles the 'routine' of a gymnast, as it appears that much attention is placed on the posture and the precision of the jumps. The high-speed recording has also revealed to what extent the behavioural is sexually dimorphic. Visual observations and recordings with standard video equipment had suggested earlier that

Male (N seq)	On perch (ms)	Jump dur. (ms)	Beard up (ms)	Jump speed (m/s)	Snap/s
#01 (4)	1488 ± 618	263 ± 16	55 ± 3	2.34 ± 1.34	0.40 ± 0.07
#02 (5)	869 ± 290	256 ± 7	54 ± 4	3.40 ± 0.08	0.85 ± 0.18
- w/f (1)	578	211	45	nd	0.87
#03 (5)	1028 ± 235	270 ± 35	42 ± 4	3.01 ± 0.18	0.49 ± 0.19
#04 (6)	771 ± 79	269 ± 10	48 ± 1	2.57 ± 0.14	0.76 ± 0.06
#05 (5)	781 ± 161	280 ± 8	52 ± 1	2.51 ± 0.13	0.67 ± 0.11
#06 (7)	515 ± 116	227 ± 21	49 ± 1	2.79 ± 0.14	0.69 ± 0.15
- w/f (1)	358	180	44	nd	1.10
#07 (6)	753 ± 341	211 ± 19	49 ± 1	2.68 ± 0.06	1.02 ± 0.21
#08 (3)	919 ± 191	270 ± 2	62 ± 1	4.02 ± 0.55	0.73 ± 0.28
#09 (3)	452 ± 76	253 ± 6	47 ± 4	5.08 ± 0.13	1.02 ± 0.22
#10 (9)	1603 ± 354	308 ± 15	59 ± 2	1.44 ± 0.14	0.37 ± 0.11
#11 (10)	891 ± 186	287 ± 8	59 ± 4	2.87 ± 0.09	0.67 ± 0.12
- w/f (2)	527 ± 83	249 ± 13	45 ± 5	2.63 ± 0.36	0.86 ± 0.18
Total	948 ± 91	266 ± 6	53 ± 1	2.85 ± 0.13	0.67 ± 0.05
$\chi^2 =$	16.4	26.6	32.5	28.1	15.1
p	0.088	0.003	0.0003	0.002	0.11

Table 1: Individual means (\pm SE) of measured variables of the snap-jump display and results of a Kruskal–Wallis anova for individual differences (DF = 10 for all tests). In rows labelled ‘w/f’, we report values for the four sequences recorded during a female’s visit to the male’s court: one sequence for male #02, one sequence for male #06 and two sequences for male #11. Values of these sequences were not used to calculate the totals and for the statistical analyses

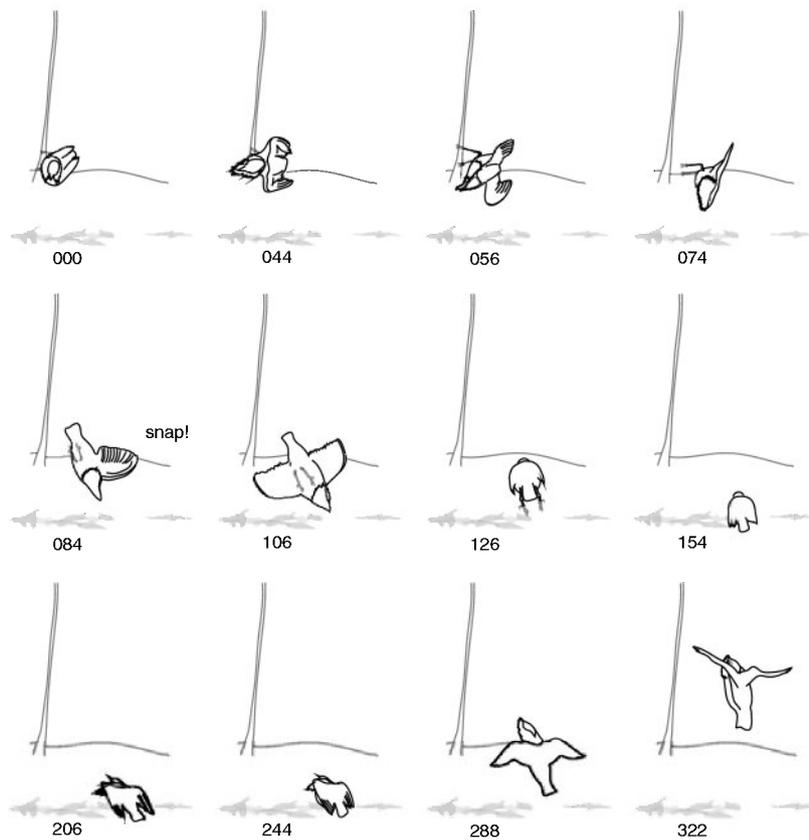


Fig. 2: A schematic representation of the grunt-jump display of a Golden-collared manakin. The male lands on the mating sapling and turns his body so that his back is directed towards the ground. Then he jumps and makes a wingsnaps while doing a cartwheel and lands on the ground with the wings partially open. After a brief pause, he takes off with a rapid vertical flight flapping the wings very fast and producing the typical grunt sound. The numbers indicated the elapsed time in milliseconds.

male and female manakins engage in a courtship dance where they make more or less the same movements, with the exception of the wingsnaps. However, the few sequences ($n = 4$) in which we could record a male and a female at the same time revealed that several aspects of the display are very different between sexes (see Supplementary Video 2). The male does not fly between saplings, he uses the wings only for the wingsnap and to turn his body before landing. The female on the contrary flies from one sapling to the other one. In addition, between jumps the male has to control his landing and to resume his 'beard up' posture, whereas the female simply perches.

Individual Differences in Courtship Displays

Among all variables, the *Beard up* reached the highest levels of significance for individual variability (Table 1). Highly significant differences were found also for the *Jump duration* and the *Jump speed*. We also evaluated the correlation between variables using non-parametric Spearman's rho corrected for multiple tests ($n = 10$) with the sequential Bonferroni correction (Table 2). The *Snap frequency* was negatively correlated with the time *On perch* and with the *Jump duration*, which were positively correlated with each other, showing that the birds that produce more wingsnaps per second perform each display sequence in a shorter time. In addition, *Beard up* was positively correlated with *Jump duration*.

Of the four sequences in which a female joined the male in the display, two were from male #11, one from male #2 and one from male #6. The values of the measured variables for these sequences are reported in Table 1 below the average values of the respective males. The few data available suggest that males display at a faster rate in the presence of females, as shown by the smaller values for *On perch*, *Jump duration*, *Beard up* and the higher number of *Snap frequency* (Table 1). The *Jump speed* could not be calculated in two cases because the males jumped to

saplings that were not used normally and therefore the distance was unknown. For male #11 *Jump speed* was lower than usual because this male in presence of a female used two saplings that were not the ones most used in all other sequences. Thus, these few videos also suggest that males modify their standard sapling use in the presence of females.

Discussion

In this study, we have analysed in details the courtship display of *M. vitellinus* using a high-speed camera. Slow-motion analyses showed that the courtship display of male manakins is an elaborate, acrobatic performance that probably requires a high level of muscular power, motor co-ordination and energy. We had shown previously that male manakins differ from birds of similar size in the mass of several groups of muscles that are used during the performance of the display (Schultz et al. 2001). Moreover, whereas observations and analyses made with standard video equipment had suggested that, with the exception of producing wingsnaps, the male and the female perform the same behavioural patterns, this study shows that the behaviour is substantially different between sexes. Thus, it seems more likely that the female follows the male in the 'dance' to observe him closely or to test his abilities rather than participating in a duet. These results are in line with our previous studies showing that the wing muscles are sexually dimorphic in this species, with male having more fast-twitch fibres than females (Schultz et al. 2001). In addition, recent work has shown that wingsnapping can be elicited in female and immature male manakins by testosterone implantation (Day et al. 2006), suggesting that sexual dimorphic displays depend partially on circulating concentrations of androgen hormones.

Quantitative analyses revealed individual differences in the duration of the jumps, the time required to reassume the beard-up posture at the end of a jump, and the speed of jumps during the snap-jump display. Repeated recordings from each male were obtained within 1–2 d; however, environmental and social conditions at the leks change rapidly and at large during the day, suggesting that the displays are consistent within individuals. Traits that differ between males could be relevant in female choice. We focused here on the first level of mate choice, i.e. the factors that influence the decision of a female to enter a male's court for having a closer look, also called courtship success. This is a very important level of selection because in *Manacus*

Table 2: Correlations (Spearman's rho) between behavioural variables. Correlation values in italics are significant after sequential Bonferroni correction for multiple tests, $\alpha = 0.05$, 10 tests

	On perch	Jump duration	Beard up	Snap/s
Jump duration	<i>0.500</i>			
Beard up	0.325	<i>0.405</i>		
Snap/s	<i>0.886</i>	<i>0.500</i>	-0.227	
Jump speed	-0.059	-0.224	-0.039	0.227

courtship and mating success are highly correlated (Stein & Uy 2006).

Behavioural components may highlight morphological traits and thus enhance male conspicuousness (Johnsgard 1994). Slow-motion analysis of *M. vitellinus* displays shows that males always turn their brightly coloured collars towards the centre of the arena. When females manakins 'asses' males while engaging in a duo dance, they usually position themselves opposite to males. Thus, if males turns their beard towards the centre of the court, they increase its relative size (i.e. the beard is closer to the female) and visibility. The action of turning back to the court's centre at the end of each jump appears to be one of the most demanding tasks of the display. The whole action resembles the landing of a gymnast after a routine, i.e. the reduction of total body momentum at touchdown (McNitt-Gray et al. 2001). In humans, such task presents a significant challenge to the neuromuscular system, because the flight time, body angular momentum and linear momentum of the total body centre of mass are determined when the gymnast departs from the apparatus; during flight, the gymnast can only control the position, velocity and acceleration of their segments (McNitt-Gray et al. 2001). Clearly similar challenges are encountered by male manakins, which use their wings to control these factors prior to landing. This leads to a second aspect on which sexual selection can act, that is, the display performance as an indicator of sensorimotor co-ordination and power and thus of condition and overall quality. Previous work has shown that courtship displays in lekking birds are energetically costly (reviewed by Andersson 1994), and the snap-jump display of *Manacus* appears a good candidate for being a particularly costly one. It is therefore not surprising that other variables that are probably associated with power and energy consumption such as jump speed and time spent jumping vary greatly between individuals.

A question raised by our results is their biological significance: do female see what males do? If the males' movements are too fast for a human observer, may be they cannot be evaluated by female manakins as well. However, manakins probably process visual information much faster than humans. Flying species need to integrate information at a higher rate than other species (Kare 1965), and in pigeons and domestic fowls the critical fusion rate (the frequency at which a flickering light source is perceived as continuous) is 2–3 times higher than in humans (reviewed in Maddocks et al. 2001).

Manakins fly very rapidly in dense rainforest and might well exceed these values. However, the signal value of the courtship display does not require necessarily the perception of each single component of the display. The selective value of the dance choreography is probably not the sum of that of each separate display element but rather depends on the balanced co-ordination of all components (see also Fusani et al. 1997).

Shorey et al. (2002) did not find a correlation between displaying behaviour and mating success in *M. manacus*. However, their study did not include a structural analysis of the behavioural traits, and some of the analysed behaviour might be more relevant for male–male competition than for female choice. Morphological traits such as the beard and collar colour are involved in both intra- and intersexual selection (Brumfield et al. 2001; McDonald et al. 2001); yet, it is not clear to which extent different displays are specifically directed to males or females. In songbirds, for example, in some species male-directed song differs considerably from female-oriented song (Catchpole & Slater 1995).

Multiple sexual display traits in manakins may serve to amplify the signals or to provide 'backup signals' (Johnstone 1996; Moeller & Pomiankowski 1993). In bowerbirds, for example, landscaping elements (i.e. bower decoration) influence the attractiveness of behavioural displays (Patricelli et al. 2003). In addition, different courtship traits may be important for different stages of female choice or for different age classes (Coleman et al. 2004). Thus, it is important that we recognize the many potential traits upon which female choice could act to characterise how sexual selections are acting on species. Using high-speed filming of the Golden-collared manakin, we have identified previously undescribed behavioural variations in male courtship displays. Further studies are required to determine the importance of display features in female choice and thus the mechanisms behind the evolution of elaborate courtship displays in manakins.

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Supplementary material

The following supplementary material is available for this article:

Supplementary Video 1: A detail of the grunt-jump display recorded at 500 frames per second and slowed down 20 times.

Supplementary Video 2: A segment of a snap-jump display recorded at 125 frames per second and slowed down 5 times. The video reveals striking differences between the movements of the male (the bird with the bright 'beard') and the female (the darker bird).

This material is available as part of the online article from <http://www.blackwell-synergy.com>.

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