RESEARCH ARTICLE

The presence of a female influences courtship performance of male manakins

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ABSTRACT
Coordinated courtship displays are a common feature of species forming long-term pair bonds. In lekking species, on the contrary, there are no stable pair bonds because partners meet only to copulate, and males indicate their quality and/or attractiveness to females by displaying morphological and behavioral traits. In some cases, females interact with these displaying males, but little is known about the role of the females in these encounters. In the Neotropical bearded manakins, females join males in their acrobatic courtship displays in the final phase of mate choice. We hypothesize that females participate in the courtship dance to better assess male motor skill by observing male responses to female signals. We filmed at high speed the courtship displays of 2 species of bearded manakins and compared the displays performed by males alone, where the female is absent from the arena, with those performed together with a female. In addition, we compared the movements of the male with those of the female and analyzed the display coordination. We found that when a female is present in the arena, males increase the speed or frequency of several performance parameters that are strongly correlated with courtship success. Additionally, males seem to pace their movements to those of the female as she takes the lead in the duo dance. Our results suggest that before choosing a mate for copulation, female manakins challenge the motor skills of prospective males.

Keywords: lek, paired courtship, motor skills, sexual selection, female preference, manakins, performance trait

La presencia de una hembra afecta el desempeño del despliegue de saltarines macho.

RESUMEN
Los despliegues de cortejo coordinados son una característica común en especies que forman lazos de pareja a largo plazo. Por el contrario, en especies con asambleas de cortejo no hay lazos de pareja estables porque la pareja se reúne sólo para copular y los machos le indican a las hembras su calidad y/o atractivo con el despliegue de rasgos morfológicos y de comportamiento. En algunos casos las hembras interactúan con los machos en despliegue, pero se sabe poco sobre el papel de las hembras en estos encuentros. Las hembras de los saltarines barbados neotropicales (Pipridae, Manacus) se unen a los machos en sus despliegues acrobáticos de cortejo durante la fase final de la escogencia de pareja. Formulamos la hipótesis de que las hembras participan en la danza de cortejo para determinar mejor las habilidades motrices de los machos al observar sus respuestas a señales de las hembras. Filmamos a alta velocidad los despliegues de cortejo de dos especies de saltarines barbados y comparamos los despliegues presentados por machos solitarios (mientras la hembra está ausente de la arena) con aquellos en los que el despliegue se hizo con la hembra. Además, comparamos los movimientos del macho con los de la hembra y analizamos la coordinación en el despliegue. Encontramos que cuando una hembra está presente en la arena, los machos incrementan la velocidad o la frecuencia de varios parámetros del despliegue que están fuertemente correlacionados con el éxito del cortejo. Además, los machos parecen ajustar el ritmo de sus movimientos con los de la hembra a medida que ella toma el liderazgo en la danza en dúo. Nuestros resultados sugieren que antes de escoger un macho para copular las hembras de los saltarines desafían las habilidades motrices de sus eventuales parejas.

Palabras clave: asambleas de cortejo, cortejo de pareja, habilidades motrices, preferencia de las hembras, rasgos de rendimiento, saltarines, selección sexual

INTRODUCTION

Mate choice in animals that form long-term pairs often involves mutual courtship. Examples of spectacular coordinated dances in the avian world include those of the Great-crested Grebe (*Podiceps cristatus*; Huxley 1914, 1923), Trumpeter Swan (*Cygnus buccinator*; Cooper 1979), and Wandering Albatross (*Diomedea exulans*; Jouventin and Lequette 1990). These coordinated displays are thought to help establish, strengthen, and maintain the pair bond, a requirement for species in which both parents contribute to raising the brood (Wachtmeister 2001). In contrast, males of species with lek mating systems contribute only sperm to the offspring, and females raise their broods alone. These males aggregate and compete for copulations by means of secondary sexual signals (Darwin 1871, Höglund and Alatalo 1995). After careful observations, females choose a male for copulation based on secondary sexual traits that indicate his quality and/or attractiveness as a mate (Lill 1974).

It is generally thought that females of lekking species do not participate in coordinated courtship displays with males (Andersson 1994). However, a few cases have been identified in which females appear to participate actively in courtship. The female Satin Bowerbird (*Ptilonorhynchus violaceus*), for example, stands in the bower, inspects it, and observes the male performing his courtship display. By crouching, she demonstrates her interest in the male, in particular the degree to which she feels threatened by his display, and the male in turn modifies his displaying intensity (Patricelli et al. 2002, Patricelli 2004). At times, female Lance-tailed Manakins (*Chiroxiphia lanceolata*) have been observed displacing males from their dance perches and then performing "back-and-forth" movements while the males make their so-called "slow flight" displays (DuVal 2007). While this kind of subtle female participation in courtship may be common, their role in courtship and mating decisions in lekking species is rarely studied. Examining a species where females engage in elaborate, coordinated displays with males may shed light on the role of female behaviors in mate choice.

We have focused our studies on the bearded manakins of the genus *Manacus* (family Pipridae). In these lekking species, females interact with males by joining them in the display before choosing their mate (Figure 1). Over an extended breeding season lasting up to 7 months, males aggregate in groups of 2–20. Between several vertical saplings, each male clears an arena on the forest floor to use for his main courtship display, the "jump-snap" display (Chapman 1935, Schlinger et al. 2013). The display consists of a series of jumps between the saplings delimiting the arena, accompanied by loud mechanical sounds, called "wingsnaps," produced by clapping wings (Bostwick and Prum 2003, Fusani et al. 2007).

Female choice in manakins consists of several stages (e.g., Lill 1974 and our own observations). In all likelihood, females are initially attracted to a lek by the noise of male wingsnaps and vocalizations. Once at the lek, the female spends time in the lower canopy to observe and, presumably, compare different males. From above, the cleared background of the arena enhances the male's plumage and behavioral signals (Stein and Uy 2006). The female eventually selects a male, descends into his arena, and the two move within the arena, remaining opposite to each other, in what has been described as a "duo dance" (Figure 1; Fusani et al. 2007). Unlike the highly coordinated displays of species such as grebes or albatrosses (Huxley 1914, 1923; Jouventin and Lequette 1990), during the dance, male and female manakins vary markedly in their behavior, with males appearing quite coordinated whereas females appear more clumsy (Fusani et al. 2007; this study). The term "duo dance" is used here to indicate this phase of the courtship during which the sexes closely interact and perform within the courtship arena. Engaging in the duo dance is the final step in the mate choice process as copulations occur at the end of the dance. In a previous study, we found that male Golden-collared Manakins (*Manacus vitellinus*) that perform certain elements of their courtship display faster (on the order of tens of milliseconds) obtain more copulations, suggesting that females have a preference for traits related to these display elements, or that they can actually distinguish the males' movements and prefer very rapid and precise movements that likely indicate his neuromuscular capabilities and overall quality as a mate (Barske et al. 2011).

Courtship success, defined here as the number of females entering a male's arena to join in the display, is a good proxy of mating success because females are more likely to dance with future sexual partners (Lill 1974, Stein and Uy 2006). There must be additional mate assessment by the female during the duo dance, however, because the probability of mating with the male at the end of the dance is only ~0.33 (data from Barske et al. 2011). By joining the male in a duo dance, the female could challenge the male to test his performance capacities and/or determine if he is able to adjust his display to her pace. A female would gain additional information on male motor skills that might be crucial for her choice of mate (see review by Byers et al. 2010). We hypothesized that female presence affects male performance and that the female functionally participates to better assess the male. If the male increases his effort in the presence of a female, one or more behavioral patterns of his display should show directional changes. Because females prefer a faster execution of certain behavioral elements of the display (Barske et al. 2011), we predicted that these elements would be performed faster in the presence of a female. In addition, if the dance were
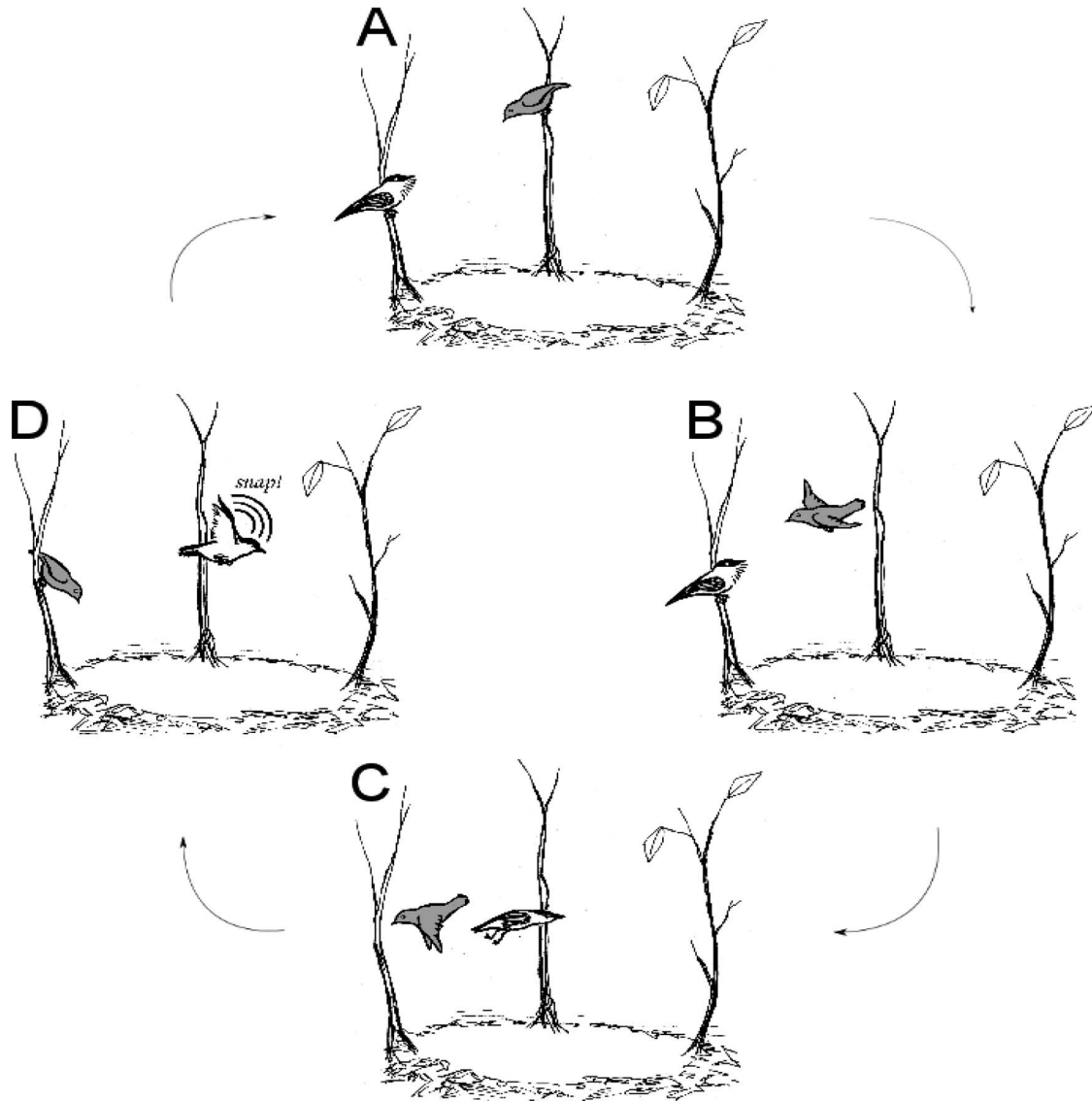
FIGURE 1. (**A**) Male and female bearded manakins (*Manacus vitellinus* and *M. candei*) in the "duo dance." To attract females, males performed courtship displays between small saplings surrounding a cleared arena. (**B**) In some cases, a female joined the male in a duo dance, which usually started as the female took off first. The female flew from one sapling to the next using, on average, 6 wingstrokes. (**C**) The male followed ~160 ms after the female, by jumping, not flying, across the arena, often producing a wingsnap in midair. (**D**) Around 100 ms after the female touched down, the male landed gracefully with his beard of elongated throat feathers exposed toward the center of the arena.

coordinated (as it appears to the naked eye), we predicted a strong temporal correlation between the movements of the two partners. Finally, if males were to adjust their display in response to the female, we predicted that females would initiate some of the coordinated movements of the dance. Here we tested these predictions in 2 species of bearded manakins, the White-bearded Manakin (*Manacus candei*) and the Golden-collared Manakin (*Manacus vitellinus*), by means of high-speed field video recordings of courtship displays.

METHODS

Using high-speed videography (MotionMeter camera, RedLake Inc., San Diego, CA, USA; 125 frames per second), courtship displays were filmed over 10 months (Feb–May 2006; Mar 2007; Mar–Apr 2008; Mar 2009; Feb–Apr 2010) from free-living animals at 2 different sites: La Selva, Costa Rica (10°26′N, 84°00′W; study species: *M. candei*) and Gamboa, Panama (9°07′N, 79°42′W; study species: *M. vitellinus*). Birds in Panama were color banded

TABLE 1. Manakin courtship display variables as previously described in Fusani et al. 2007 and Barske et al. 2011. "Yes" and "no" indicate whether the variable is performed or not during the "duo dance" by each sex. While males jumped between saplings using their wings for the production of wingsnaps only, females flew to compute the same distance.

Variable name	Variable description	Performed in duo dance	
		Male	Female
On Perch	time spent on a sapling between 2 jumps	yes	yes
Jump Duration	time spent in air	yes	yes
Jump Speed	distance between 2 saplings divided by Jump Duration	yes	yes
Wingsnap Frequency	number of wingsnaps per second	yes	no
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 in which the feet touch the landing sapling to the freezing of the posture	yes	no
Jump Interval	interval between 2 jumps; thus the sum of Jump duration and On perch	yes	yes

for individual recognition; in Costa Rica, birds were identified by their courts, which males defend aggressively during the courting season (McDonald et al. 2001). Over more than 15 years of observations of bearded manakins, we have never seen an adult intruder entering and displaying in an arena without being attacked by the owner of the court.

The camera was placed 5 m from the arena and controlled remotely. Slow motion analysis of videos was performed using The Observer Video Pro 4.0 (Noldus Information Technology, Wageningen, The Netherlands; Fusani et al. 2007, Barske et al. 2011). The behavioral variables of the courtship display were described and quantified (Table 1); *Wingsnap frequency*, *On perch*, and *Beard up* have been shown to play a primary role in female choice (Barske et al. 2011).

To investigate the effects of female presence on male display performance, we analyzed video sequences in which a male displays alone and is subsequently joined by a female. Thus, each display sequence was divided into 3 periods: before the female joins the male (preF), while the female displays with the male (withF), and after the female has left (postF). The green-colored females can be difficult to observe in the forest; therefore, when the female is not in the arena itself we do not always know if she is still within the lek or has departed the vicinity.

Finally, to study if movements were coordinated between partners and if males adjust their behavior in response to the movements of the females, we investigated the temporal relationships between behavioral variables that were similarly displayed by both males and females (Table 1). To determine which sex takes the lead in the display, we identified the jumping order and measured latencies between the male and the female at the beginning and end of each jump.

Statistical Analyses
We used SPSS 19 (IBM) for statistical analyses. We used a mixed-model design with normal distribution to test for

effects of female presence on the display. Videos (of individual displays) were nested within males, and to control for species differences, species as well as the interaction between species and female presence were included as fixed factors. Pairwise comparisons using Bonferroni adjustments for multiple comparisons were used to compare data before, during, and after female presence based on average values of the 2 species combined. To compare male and female behavior, we used a mixed-model design with normal distribution. Videos were nested within each male and female pair. To control for species differences, species as well as the interaction between species and sex were included as fixed factors.

To understand if there was a relationship between male and female behaviors, we performed a multiple regression analysis with the male behavior as the dependent variable, and female behavior, species, and male identity (the identity of females was unknown) as predictor variables using the stepwise criterion selection method. The introduction of the male identity in the model as a predictor variable was used to remove the effects of the replicates from a same individual because our main question here was whether male and female behavior are correlated and not whether there are differences between males (Bland and Altman 1995).

We used Pearson's chi-square test to investigate if one of the sexes initiated and ended the jumps before the other sex. We investigated if the female starts a jump more often than a male by comparing the number of times a female starts the jump (observed values) with the number of times a male starts the jump (expected values if males and females were to start a jump the same amount of times). A paired t-test was used to investigate if females displaced males or not. Here we compared 2 variables: the number of times the female did not displace the male (independent) and the number of times the female did displace the male (dependent), and the factor was the single courtship dance (one per individual male). We report the statistical effects of the species on our analyses; however, species differences will
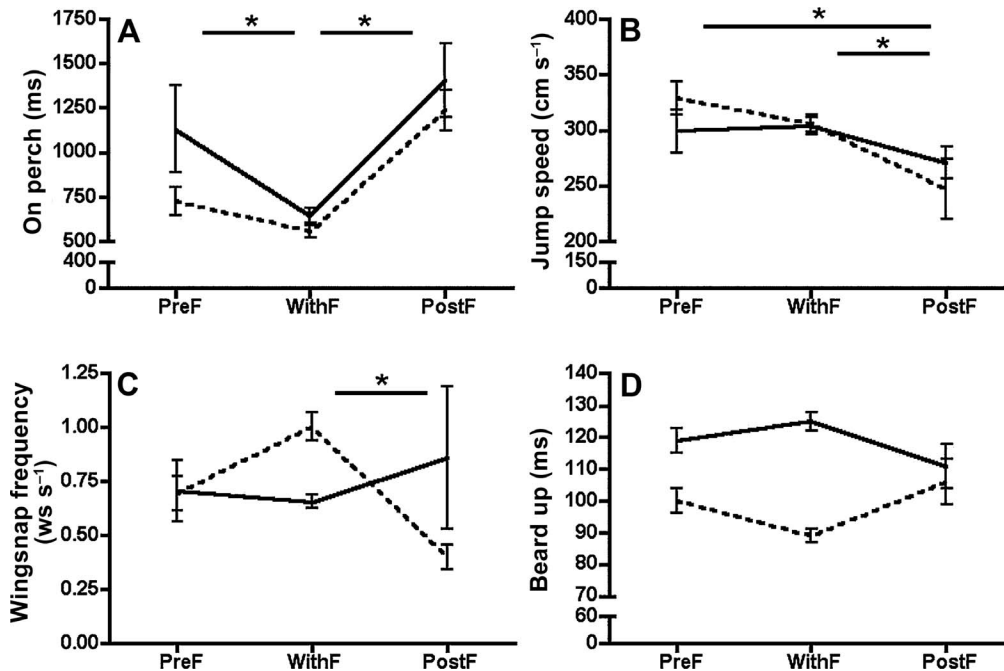
FIGURE 2. Male manakin courtship performance before, during, and after the presence of a female: (**A**) *On perch* significantly decreased during female presence ($F_{2,78} = 9.57$, $P < 0.001$). (**B**) *Jump speed* significantly decreased once the female left the arena ($F_{2,87} = 7.34$, $P < 0.01$). (**C**) *Wingsnap frequency* was significantly affected by female presence ($F_{2,83} = 4.53$, $P = 0.01$). (**D**) We found a significant interaction effect of female presence and species on *Beard up* (interaction effect: $F_{2,72} = 7.66$, $P < 0.01$) as well as a significant effect of species ($F_{1,24} = 18.67$, $P < 0.001$). When species where analyzed separately, we found a significant effect of female presence on *Beard up* in *M. candei* ($F_{2,29} = 5.23$, $P = 0.01$). There was no effect of female presence on *Beard up* in *M. vitellinus* ($F_{2,45} = 2,95$, $P = 0.06$) or across the 2 species ($F_{2,72} = 0.35$, $P = 0.71$).

be addressed in more detail in a separate publication. The Shapiro-Wilk test was used to investigate the normality of the data. *On perch, Beard up, Wingsnap frequency,* and *Jump Interval* were log transformed to obtain normality, and a Gaussian distribution was specified in analyses of this data. Data in the text are given as mean ± SEM.

RESULTS

Effects of Female Presence

For 25 males (8 *M. candei* and 17 *M. vitellinus*) we obtained up to 3 (2.0 ± 0.1) video recordings in which we could compare behavior before a female entered the arena with that recorded while she was in the arena and immediately after she departed. Only a few videos with copulations were obtained, so duo dances that ended in a copulation were excluded from this analysis. Males significantly reduced their time *On perch* when the female was present; that is, they paused on saplings for 613 ± 31 ms compared to 986 ± 161 ms before she entered the arena and 1315 ± 112 ms once she had departed (female presence: $F_{2,78} = 9.57$, $P < 0.001$; species: $F_{1,15} = 2.01$, $P = 0.18$; interaction: $F_{2,78} = 0.80$, $P = 0.46$; post hocs: preF vs. withF: $P = 0.04$; preF vs. postF: $P = 0.06$; withF vs. postF: P

< 0.001; Figure 2A). In addition, *Jump speed* significantly decreased once the female departed the arena (female presence: $F_{2,87} = 7.34$, $P < 0.01$; species: $F_{2,23} = 0.19$, $P = 0.66$; interaction: $F_{2,87} = 1.49$, $P = 0.23$; post hocs: preF vs. withF: $P = 1$; preF vs. postF: $P < 0.01$; withF vs. postF: $P < 0.01$; Figure 2B). *Wingsnap frequency* was significantly higher in the presence of the female compared to when she left the arena (female presence: $F_{2,83} = 4.53$, $P = 0.01$; species: $F_{1,25} = 0.000$, $P = 0.99$; interaction: $F_{2,83} = 3.46$, $P = 0.04$; post hocs: preF vs. withF: $P = 0.14$; preF vs. postF: $P = 0.69$; withF vs. postF: $P = 0.03$; Figure 2C). *M. candei* decreased *Wingsnap frequency* after the female left, whereas *M. vitellinus* did not. There was a significant interaction effect of female presence and species on *Beard up* (interaction effect: $F_{2,72} = 7.66$, $P < 0.01$; Figure 2D) as well as a significant effect of species ($F_{1,24} = 18.67$, $P < 0.001$). When species where analyzed separately, we found a significant effect of female presence on *Beard up* in *M. candei* ($F_{2,29} = 5.23$, $P = 0.01$). *Beard up* was significantly faster when the female was present compared to when she left the arena (post hocs: preF vs. withF: $P = 0.10$; preF vs. postF: $P = 0.93$; withF vs. postF: $P = 0.02$; Figure 2D). There was no effect of female presence on *Beard up* in *M. vitellinus* ($F_{2,45} = 2.95$, $P = 0.06$).

Male and Female Movements and Their Coordination

High-speed videos revealed that the movements of the females differ substantially from those of the male; while the males jumped (and did not fly) between saplings using their wings for the production of wingsnaps only, females flew using on average 6 wing strokes to achieve the same distance (Figure 1). Males also took extraordinary care in restoring their posture at the end of each jump, with the beard well exposed, while females did not show any unusual posture upon landing (Table 1; Fusani et al. 2007).

From recordings of 17 males displaying with a female, we obtained 171 measures of the following behavioral variables that could be directly compared between sexes: *Jump duration*, *On perch*, and the interval between 2 jumps, *Jump interval*, which was the sum of consecutive *On perch* and *Jump duration* units (Table 1). Males needed 7% less time than females to cross the arena; in other words, males spent on average 22 ms less time in the air (*Jump duration* [Figure 3A]: sex difference: $F_{1,326} = 10.06$, $P = 0.002$; species: $F_{1,15} = 0.59$, $P = 0.45$; interaction: $F_{1,326} = 1.08$, $P = 0.30$). There was not a sex difference in the amount of time spent on saplings between 2 jumps (*On perch*), nor was there a sex difference for *Jump interval*, but in both cases *M. candei* required significantly less time to jump again than *M. vitellinus* (*On perch* [Figure 3B]: sex difference: $F_{1,323} = 0.12$, $P = 0.73$; species: $F_{1,11} = 0.01$, $P = 0.03$; interaction: $F_{1,323} = 0.13$, $P = 0.72$; *Jump interval* [Figure 3C]: sex difference: $F_{1,321} = 0.29$, $P = 0.59$; species: $F_{1,11} = 7.37$, $P = 0.02$; interaction: $F_{1,321} = 0.00$, $P = 0.99$).

To understand if males adjusted their courtship to the female's behavior, we studied the regression between male and female *Jump duration*, *On perch*, and *Jump interval* within displays (Table 1).

For male *On perch*, the regression model with female *On perch* as the only predictor variable was highly significant (adjusted $R^2 = 0.77$, $F_{1,170} = 551.08$, $P < 0.001$; Figure 4A), and the standardized beta coefficient for female *On perch* was large and highly significant (0.88, $t = 23.48$, $P < 0.001$), whereas betas for both male identity (ID) and species were small and nonsignificant (ID: 0.07, $t = 1.85$, $P = 0.07$; species: 0.04, $t = 0.91$, $P = 0.36$). Thus, the duration of the time on perch between jumps for males was strongly correlated to the time on perch of their female display partners. Similarly, the main predictor of male *Jump interval* was female *Jump interval* (adjusted $R^2 = 0.77$, $F_{1,170} = 562.50$, $P < 0.001$; Figure 4B), and the standardized beta coefficient for female *Jump interval* was large and highly significant (0.88, $t = 23.72$, $P < 0.001$), whereas betas for both male ID and species were small and nonsignificant (ID: 0.05, $t = 1.43$, $P = 0.15$; species: 0.05, $t = 1.28$, $P = 0.20$). Male *Jump duration*, on the contrary, was not predicted by either female *Jump duration*, male ID, or species (adjusted $R^2 = 0.003$, $F_{1,170} = 1.15$, $P < 0.33$; beta
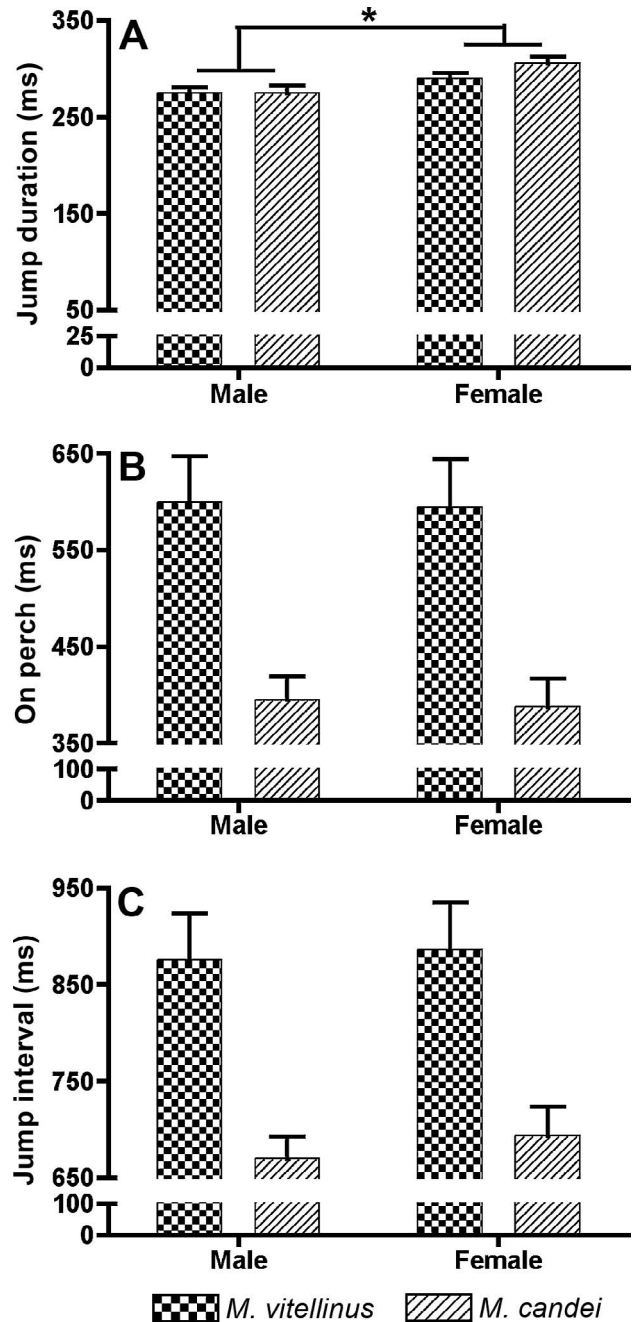

FIGURE 3. Comparisons of behaviors (mean ± SEM) performed by both males and females in the manakin courtship display: *Jump duration*, *On perch*, and the interval between 2 jumps, *Jump interval*, which was the sum of consecutive *On perch* and *Jump duration* units (Table 1). (**A**) Males jumped faster than females fly (*Jump duration*: $F_{1,326} = 10.06$, $P = 0.002$). (**B**) There was no difference in amount of time spent on saplings between 2 jumps (*On perch*: $F_{1,323} = 0.12$, $P = 0.73$). (**C**) There was no difference in the *Jump interval* between males and females ($F_{1,321} = 0.29$, $P = 0.59$).
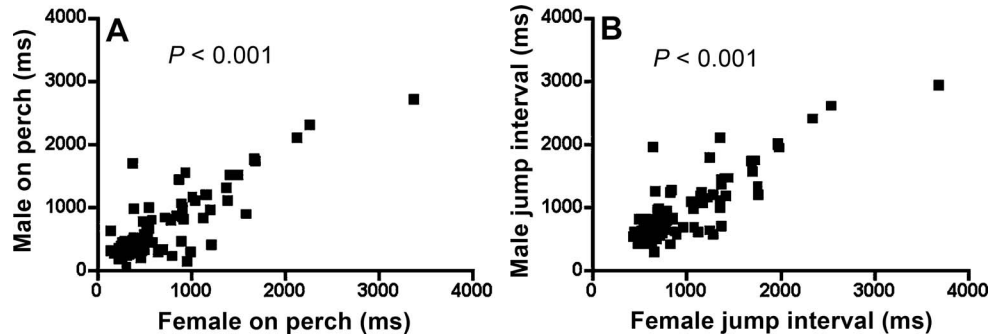
FIGURE 4. Coordination of courtship between males and females: (**A**) There was a significant relationship between males and females for *On perch* (adjusted $R^2 = 0.77$, $F_{1,170} = 551.08$, $P < 0.001$) as well as for (**B**) *Jump interval* (adjusted $R^2 = 0.77$, $F_{1,170} = 562.50$, $P < 0.001$).

coefficients: *Jump duration*: 0.14, $t = 1.76$, $P = 0.08$; ID: 0.05, $t = 0.71$, $P = 0.48$; species: 0.02, $t = 0.27$, $P = 0.79$).

A significant positive correlation per se does not explain whether the males adjust their movements to the females or vice versa; however, we found that females start each movement more often than males (Figure 5). Females were the first to start a jump 92.6% of the time (5.6 ± 0.5 of 6.1 ± 0.6 jumps), leading by 160 ± 20 ms (chi-square test: $\chi^2 = 30.800$, df = 9, $P < 0.001$), and were more often the first ones to land, 100 ± 10 ms before the male, after each movement ($\chi^2 = 27.94$, df = 9, $P < 0.01$). Thus, the female took the temporal lead in the duo dance. Furthermore, the female appeared to displace the male from his position; 74% of the female jumps were targeted toward the position of the male, which resulted in the male abandoning his position ($t_{13} = 2.37$, $P = 0.03$).

DISCUSSION

The presence of a female in a male manakin's arena, together with her participation in his courtship display, affects several features of the male's courtship display performance. First, with a female present, males reduce their pause between jumps, a trait previously found to be correlated with female preference; males that remain perched longer between 2 successive jumps have signifi-

cantly lower mating success (Barske et al. 2011). Whereas the frequency of wingsnaps increases in the presence of the females, the speed of the male's jump decreases once the females departs. Based on previous findings (Barske et al. 2011), these results suggest that males enhance their behavioral performance at a period most crucial for mate choice, just prior to arrival of the female or only when the female is present, to increase the likelihood of obtaining a copulation (Lill 1974, Stein and Uy 2006). At the same time, our results indicate that females "test" males by pacing their courtship. High-speed videography reveals that the female takes the temporal lead role during the duo dance, suggesting that the males coordinate their movements between the saplings with those of the females. Video footage also shows clearly that females fly between saplings while males jump. Thus, males use only their leg power to cover the same distances covered by females, who use both their legs and wings. Males differ further from females in that they perform a powerful wingsnap during the jump, and they carefully control their posture upon landing. Thus, males utilize extraordinary neuromuscular coordination, motor skill, and muscle power to keep pace with the females. We also identified some species differences in courtship behavior, which will be the subject of a more extensive future report (Barske et al. personal communication).
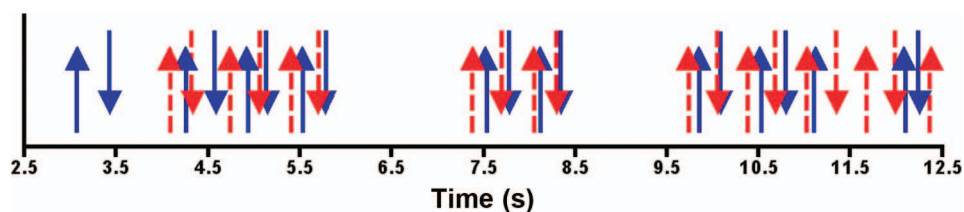

FIGURE 5. Females lead the "duo dance": Females usually lead the duo dance as shown in this scheme describing a representative example of male and female jumps along a timeline. The male is indicated by the blue arrows (upward arrow = starts the jump; downward arrow = lands), the female by the red arrows. During the duo displays, the male and the female performed almost simultaneous jumps, and it was the female that paced the jumps. The sequence stopped when the female left the arena (last red upward arrow).

Paired courtship, including coordinated dances and song duetting, has been described in many species that have long term relationships, and their suggested function includes phenotypic matching as well as strengthening of pair bonds (Wachtmeister 2001). In lekking species, females are generally thought to function as observers, often watching several displaying males simultaneously (e.g., Greater Sage-Grouse [*Centrocercus urophasianus*; Gibson 1996], Ruff [*Philomachus pugnax*; Hill 1991], and Black Grouse [*Tetrao tetrix*; Rintamaki 2000]); a participatory role in the courtship display itself is rarely considered. In contrast, studies of some species indicate that signals from the female alter male courtship. Examples include the female Satin Bowerbird and the Lance-tailed Manakin (described above; Patricelli et al. 2002, Patricelli 2004, DuVal 2007).

To our knowledge, bearded manakins are the first lekking birds in which coordinated movements between males and females during courtship have been described. The coordination might play a role in phenotypic matching (i.e. a mechanism allowing the assessment of genetic relatedness), but because only a few males obtain most of the copulations, it seems unlikely that this is the major driver for the duo dance. Rather, we suggest that during the duo dance, females increase their knowledge about a potential mate. Males would benefit from such a mechanism because they would perform at their maxima only to females who demonstrate strong interest and are likely candidates for a successful mating (Andersson 1994).

Similar energy saving strategies have been suggested for Cassin's Finch (*Haemorhous cassinii*) males that increase efforts to attract females by only singing when females are absent (Sockman et al. 2005) and for male Zebra Finches (*Taeniopygia guttata*) that adjust song amplitude in response to female distance (Brumm and Slater 2006). By challenging male courtship displays, females might directly test male motor skill (Byers et al. 2010) and indirectly test additional physiological capabilities. For example, female manakins seem able to distinguish subtle differences (on the order of centiseconds) in the performance of certain moves of the male's display (Barske et al. 2011). Presumably, accurate performance of intricate moves at high rates of speed requires outstanding motor skill of individual males. Moreover, we have found that during courtship displays, male heart rates accelerate from ~500 to >1000 beats per minute (Barske et al. 2011); thus, courtship might indirectly reflect optimal cardiovascular function (Clark 2012). This hypothesis has been suggested for other species as well. A positive correlation between signal honesty and female proximity has been shown for running agility in the pronghorn (*Antilocapra americana*; Byers 1997), complexity of calls in the tungara frog (*Physalaemus pustulosus*, Akre and Ryan 2011), color darkness in common minnows (*Phoxinus phoxinus*;

Kekäläinen et al. 2010), and carotenoid-based bill color in Zebra Finches (Gautier et al. 2008).

Other hypotheses of why males adjust their behavior in response to female behavior come from studies of bowerbird courtship. It has been proposed that females signal to males when they are unthreatened by their displays; males receiving such signals can then increase display intensity further enhancing their chance for success (Patricelli et al. 2002, 2006). We have never observed forced copulations in manakins; thus, this argument is an unlikely explanation for males adjusting to female pace in these species. Other studies have shown that females can signal receptivity using pheromones (Maxwell et al. 2010), acoustic signals (Balsby and Dabelsteen 2002), and behavioral signals (e.g., Guillermo-Ferreira and Bispo 2012). A female manakin signals receptivity to copulation by joining the male in the display. Males perform a unique "grunt" display, a half-flip somersault followed by a noisy vertical flight, to which receptive females respond by perching on his "mating sapling" (Lill 1974, Coccon et al. 2011). Thus, it seems unlikely that the duo dance has the sole function of signaling female sexual receptivity. If females simply wanted to signal their receptivity, they could directly land on that sapling without engaging in the courtship display before and avoid possible costs of the display.

Manacus females may incur a cost by participating in courtship. In males, heart rates rise to extremes during courtship, but because females do not wingsnap and fly rather than jump, they probably suffer less energetic costs than do the males. Females still invest time, however, and probably increase their predation risk during the dance. Females of other manakins can avoid such costs, especially in species where multiple males perform coordinated courtship displays (Trainer and McDonald 1995, DuVal 2007, Anciaes and Prum 2008). In the Lance-tailed Manakin, for example, by simple observation, females can assess the attractiveness of an alpha male when he is challenged by a beta male, thus limiting her need to participate. In these birds, females only periodically participate in courtship with males, unlike the group of bearded manakins (DuVal 2007).

Our previous studies of *M. vitellinus* males courting in the absence of a female showed that males who spent less time *On perch* produced faster *Beard up* elements and a greater frequency of wingsnaps and had greater reproductive success (Barske et al. 2011). In this study we found that males increased their *Wingsnap frequency* while the female was present compared to when she left the arena. Moreover, in this study we found that *Jump speed* increased with female presence. These slight differences across studies may reflect the greater time resolution over which behaviors were analyzed with respect to the behavior of the female in this analysis.

Alternatively, it might be that males optimize specific behaviors depending on the position of the female. For example, females may only be able to evaluate *Jump speed* when close to the arena, when she is adjacent to the male. *Jump speed* might then be more important to females in making a mating decision, whereas other behaviors may influence their decision to join the male. Greater Sage-Grouse females show a similar pattern in that visits are related to acoustical components of the male's display, whereas mating is related to display rate (Gibson 1996). We cannot exclude the possibility that males practice when they are alone and produce a more optimal display when the female is present, similar to finches switching from undirected to female-directed songs (Woolley and Doupe 2008). Finally, by coordinating his moves with the female, a male might maintain an optimal position with respect to her, increasing the visibility of the bright color of his beard and collar (Uy and Endler 2004, Stein and Uy 2006), thereby maximizing the efficiency of his multimodal signaling to the female (Candolin 2003). No doubt a variety of subtle sensory and motoric variables influence the ultimate performance of the duo dance.

Maynard Smith (1956) noted that female *Drosophila subobscura*, a species of fruit fly, may challenge males' reflexes in coordinated displays. Our study suggests a similar mechanism. We have no direct evidence that females prefer more coordinated dancers, but this idea is certainly suggestive. In fact, the displays of manakins are an elaborate mix of acrobatics, landscaping, exposing bright plumage, and perhaps learned dance routines (as suggested by the study of Coccon et al. 2011). Females might base their choice on an integrated aesthetic value of the display, a value to which coordination of limbs and control of body posture contribute substantially. In this sense, we agree with other authors (Prum 2012) that elaborate courtship displays might have evolved via Fisherian sexual selection on females' intrinsic aesthetic value that the analysis of each separate component will inevitably fail to discover.

In summary, the reasons for the active involvement of females in courtship behavior in *Manacus* and in other lekking species would benefit from additional study. Such studies could shed new light on the behavioral ecology of individual species as well as augment our understanding of mating systems more generally.

ACKNOWLEDGMENTS

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