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COOPERATIVE DISPLAY AND LEKKING BEHAVIOR OF THE LANCE-TAILED MANAKIN (*CHIROXIPHIA LANCEOLATA*)

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ABSTRACT.—Male Lance-tailed Manakins (*Chiroxiphia lanceolata*) perform multi-male courtship displays for females. To characterize the behavioral repertoire and the lek spatial organization of this species, I observed lekking males on Isla Boca Brava, Chiriquí Province, Panamá. Breeding began in March and continued through June, though courtship displays were recorded as late as November. Males were active throughout the day at display areas on the dispersed lek. Display areas were spaced 102 ± 30 m apart and averaged $2,480 \pm 1,060$ m² in area (range: 525–4,500 m²; $n = 24$ display areas). The behavioral repertoire of Lance-tailed Manakins included 11 dance display elements, 7 common vocalizations, and 2 types of male–male duet songs. Duet songs and multimale dances for females were cooperative efforts by male pairs and included display elements that were never performed during courtship displays by solitary males. However, males performed both cooperative and entirely solo displays for females that ended in successful copulation, which suggests that cooperation is not obligate in this species, at least on the level of individual displays. Two sonations, or nonvocal communicative sounds, were noted during courtship displays: low-amplitude pulses of noise produced in rapid sets of 7–30 clicks during slow flight displays, and a low-frequency *woosh* produced at the nadir of swoop displays. The Lance-tailed Manakin display repertoire provides information useful in comparative analyses of the origin and evolution of display behavior within the manakin clade and in studies of the adaptive consequences of individual behavior within this species. *Received 9 November 2005, accepted 23 October 2006.*

Key words: *Chiroxiphia lanceolata*, display behavior, Lance-tailed Manakin, lek, mechanical sound.

Exhibición Cooperativa y Comportamiento de Asambleas de Cortejo en *Chiroxiphia lanceolata*

RESUMEN.—Los machos de *Chiroxiphia lanceolata* realizan exhibiciones de cortejo entre varios individuos para atraer a las hembras. Para caracterizar el repertorio de los comportamientos y la organización espacial de las asambleas de cortejo de esta especie, observé a machos en la Isla Boca Brava, provincia de Chiriquí, Panamá. La reproducción comenzó en marzo y continuó durante todo junio, aunque los despliegues de cortejo fueron observados hasta noviembre. Los machos presentaron actividad durante todo el día en las áreas de exhibición dentro de la asamblea de cortejo dispersa. Las áreas de exhibición estuvieron separadas por 102 ± 30 m y en promedio tuvieron un tamaño de $2,480 \pm 1,060$ m² (rango: 525–4,500 m²; $n = 24$ áreas de exhibición). El repertorio de comportamientos de *C. lanceolata* incluyó once elementos de exhibición de danza, siete vocalizaciones comunes y dos tipos de cantos en dueto entre machos. Los cantos en

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dueto y las danzas entre machos realizados para atraer a las hembras fueron esfuerzos cooperativos por parte de parejas de machos e incluyeron elementos de exhibición que nunca fueron realizados en exhibiciones de cortejo realizadas por machos solitarios. Sin embargo, los machos realizaron exhibiciones tanto cooperativas como totalmente solitarias para las hembras, y en ambos casos éstas terminaron en cópulas exitosas. Esto sugiere que la cooperación no es un comportamiento obligatorio en esta especie, por lo menos a nivel de las exhibiciones individuales. Dos sonidos comunicativos no vocales fueron registrados durante las exhibiciones de cortejo: pulsos de ruido de baja amplitud producido en conjuntos rápidos de 7–30 clics durante las exhibiciones de vuelo lento, y un *uuush* de baja frecuencia producido en el nadir de las exhibiciones de vuelo en picada. El repertorio de exhibiciones de *C. lanceolata* provee información que es útil para análisis comparativos sobre el origen y la evolución del comportamiento de exhibición en el clado de los pípridos y para estudios sobre las consecuencias adaptativas del comportamiento individual en esta especie.

Cooperative courtship is a rare form of mate attraction that involves coordinated behaviors among pairs or groups of males. Coordinated male displays are found in several avian families but are most widespread among the Neotropical manakins (family Pipridae). Within this family, males of at least five genera perform coordinated displays on lek territories for cooperative or competitive purposes (Prum 1994). Coordinated displays are considered cooperative when synchronized activities of males increase the reproductive success of only certain individuals in the group: subordinate males effectively forego reproduction while helping their dominant partners attract mates. Within the manakin genus *Chiroxiphia*, all species studied to date display cooperatively, and cooperation is considered obligate for mating to occur (Blue-backed Manakin [*C. pareola*], Snow 1963, Sick 1967; Long-tailed Manakin [*C. linearis*], Foster 1977; Swallow-tailed Manakin [*C. caudata*], Foster 1981). These displays have drawn considerable attention because of the apparently paradoxical occurrence of cooperation in a situation characterized by intense sexual competition.

Courtship in *Chiroxiphia* consists of both cooperative song and dance displays. Cooperative songs are closely synchronized duets sung by two or more males in a group display area (Trainer and McDonald 1993). When a female is present, the primary male pair executes an elaborate dance on a low display perch (Slud 1957, Snow 1963). If the female is receptive, only one male—the alpha—remains to complete the courtship and mate (Foster 1981, McDonald 1989a). Studies of *Chiroxiphia* spp., in particular the Long-tailed Manakin, have provided much

of our current knowledge concerning the phenomenon of cooperative courtship (Cockburn 1998, Krakauer 2005).

The Lance-tailed Manakin (*C. lanceolata*) also has cooperative courtship displays. The displays of this species were briefly described during an avifauna survey in the lowlands of northeastern Venezuela (Friedmann and Smith 1955) and through short-term observation of unbanded males in Ibagué, Colombia (Pacheco and Laverde 2002). However, there has been no comprehensive characterization of male displays in this species and, in particular, no description of display behavior when females are present.

Lek spatial organization, display characteristics, and sonations (i.e., nonvocal acoustic signals produced during display; Bostwick and Prum 2003) are all hypothesized to have a strong phylogenetic component in the manakin clade (Prum 1994, 1998; Bostwick 2000). However, the resolution of phylogenetic analyses of behavior is compromised by the fact that behavioral data for many species are lacking or limited to short-term observations that likely fail to capture the full behavioral repertoire of a species. Here, I describe the vocalizations, sonations, and courtship behaviors of the Lance-tailed Manakin. I also characterize seasonal and daily timing of activity on display territories as well as spatial distribution and characteristics of display sites. The resulting characterization provides detailed information that will be useful both in future phylogenetic comparisons and in studies of the adaptive consequences of individual behavior within this species.

METHODS

Study site.—The study was carried out in a 46-ha area at the eastern end of Isla Boca Brava, Chiriquí Province, Republic of Panamá (8°12'N, 82°12'W; Fig. 1). Rainfall at this site is concentrated during a seven-month rainy season, from May to November. Vegetation consists mostly of secondary-growth deciduous tropical forest with an understory of saplings and shrubs including *Piper* spp. (Piperaceae), *Capparis frondosa* (Capparidaceae), *Hirtella racemosa* (Chrysobalanaceae), *Acacia* spp. (Mimosaceae), species of Euphorbiaceae, and *Aphelandra* spp. (Acanthaceae). Approximately 10 ha of the site have been cleared for housing development. The study was conducted for a total of 16.5 months from 1999 to 2004 (Table 1).

Study animal.—The Lance-tailed Manakin is a small (approximately 15.5–22 g), mostly frugivorous bird that occupies the Pacific lowlands of southwestern Costa Rica and western Panama and the Caribbean lowlands of Colombia and Venezuela up to an elevation of ~1,700 m

(Wetmore 1972, Ridgely and Tudor 1994). Males and females are sexually dichromatic, and males exhibit age-related plumage stages, first exhibiting definitive plumage in the breeding season of their fourth year (DuVal 2005).

The conspicuous songs and dances of male Lance-tailed Manakins are performed on traditional “display areas.” Display areas are occupied by two to eight regularly observed males, one pair of which performs courtship displays for females (display areas are analogous to “perch zones” of Long-tailed Manakins; McDonald 1989a), and a lek in this species is the assemblage of display areas that females may visit to observe potential mates (see below). Display areas remain stable in location for multiple years, even when the males attending them change. Each display area includes multiple trees in which resident males perch to perform duet songs, and one or more “display perches,” which are horizontal branches or saplings on which males perform displays.

Terminology.—Duet song and dance displays are distinct and together comprise the

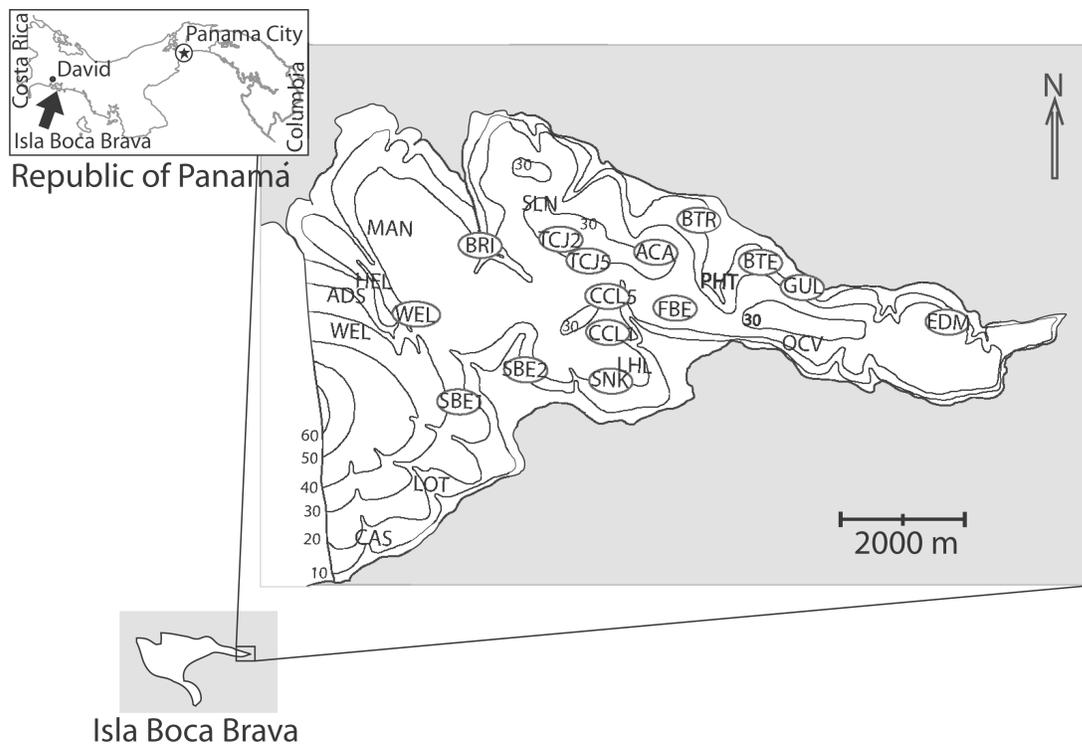


FIG. 1. Map of study site. Three-letter abbreviations indicate display areas that persisted for more than one field season. Circled sites were observed two to three times per week throughout the study. Lines indicate 10-m contours.

TABLE 1. Observation effort on the Isla Boca Brava study site.

Year	Field-season dates (start to stop)	Number of focal display areas	Number of observation hours	Observation schedule (h session ⁻¹)	Number of months in field season
1999	11 June–20 July	–	0	0	1
2000	12 March–30 June	13	639	2	4
2001	8 March–30 June 16–29 November	15 7	1,109 46	2 2	4 0.5
2002	28 February–30 June	18	1,805	2	4
2003	19 March–13 May	16	420	0.5–2	2
2004	21 March–12 April	14	173	0.5–2	1

Notes: Focal display areas are group territories at which frequent, scheduled observations were conducted throughout the field season. Focal areas were observed two times per week in 2000–2001 and three times per week in 2002–2004, and 17 unique focal areas were observed for three or more years of the study. No formal observations were conducted in 1999, but mist-netting effort in that year enabled later behavioral observations of banded individuals. I assessed activity in the apparent nonbreeding season from 16 to 29 November 2001.

Lance-tailed Manakin's display repertoire. The stereotyped behaviors that make up these variable displays are here called "display elements." When vocalizations and individual display elements were apparently homologous to those described by other researchers, I used these previous names. When homology was uncertain or clear behavioral differences existed, I noted similar displays but did not use the same names.

Capture and marking.—Lance-tailed Manakins were captured using mist nets set in areas of high manakin activity, primarily display sites and near fruiting trees. Captured animals were marked with a unique combination of three colored plastic leg bands and one numbered aluminum band. Birds were sexed using either plumage and brood-patch characters or genetic data, described in detail elsewhere (DuVal 2005). Between 1999 and 2004, 457 postfledging individuals were captured on the study site during a total of 2,155 mist-net hours (one mist-net hour = one 12-m net open for 1 h). An additional 132 individuals were banded as nestlings.

Nest searching and monitoring.—Nests were located by regular and thorough inspection of understory vegetation throughout the study site. Nests were monitored every two days until nestlings fledged or nest contents disappeared. The timing of nest initiations is one indicator of the duration of the breeding season. Nest-initiation date was determined by direct observation of the appearance of an egg in a previously empty nest, or by extrapolation of laying date given 18 incubation days and 16 nestling days required before fledging (E. H. DuVal unpubl. data).

Spatial analysis and display-area measurements.—I quantified display area location by plotting the positions of observed display perches on a 1:2,000 scale map of the study site and recording the location of the most frequently used display perches using a global positioning system (GPS) unit. Twenty-four display areas were stable in location for three or more years of the study. I estimated the average distance between these areas by mapping display perches in ARCVIEW GIS, version 3.2 (ESRI, Redlands, California), after which I used the program DIVA-GIS, version 4.0 (Hijmans et al. 2004), to calculate the distance between the main display perches in neighboring display areas. I plotted the location of display perches and trees regularly used for duet singing and used a 100% minimum-convex-polygon estimate of these points to calculate area of display territories in ARCVIEW. Distances between display areas were measured from center to center of adjacent areas. To characterize display perches, the diameters of 13 regularly attended perches were measured using dial calipers (± 0.1 mm), and the vertical heights of these perches were measured with a measuring tape (± 0.5 cm).

Behavioral observations.—Seventeen display areas were designated as focal areas and were observed two to three times per week for at least three field seasons. Twenty-six other display areas were observed less frequently. Observations were conducted between 0700 and 1800 hours (Standard Time) during all months of field research conducted after 1999, for a total of 4,192 observation hours (Table 1). Observation sessions were usually 2-h periods

of continuous monitoring (one-hour and half-hour sessions were conducted in 2003 and 2004). Observers recorded number and type of vocalizations, identity and plumage of birds present, male song rate, male–male interactions, and frequency and details of courtship displays. When exact durations of these display components could not be recorded, observers scored the occurrence of each. Duetting song bouts were considered to have ended when one male left the area or both males were silent for >15 s. Dance displays were considered to be for females when a female perched on the display perch during the dance. Observers sat quietly 8–12 m from a focal display perch; observer movements were limited to those necessary to read band combinations of duetting or dancing birds. The schedule of observations was predetermined weekly to ensure that sampling was independent of current activity.

The sequence of courtship-display elements was analyzed using particularly detailed observations of 16 displays that ended in copulations or copulation attempts. These were displays for which observers recorded the order and timing of all transitions from one display element to another. In all cases, observers had at least one complete field season of experience recording Lance-tailed Manakin displays prior to data collection. Transitions between display elements were tallied in a transition matrix. The percentage of instances in which one display element followed the other was calculated by summing rows and calculating a per-row percentage for each possible subsequent display. Sample sizes precluded significance testing of transition probabilities. Instead, I present a schematic diagram of the display sequence with arrows linking elements that followed the preceding element >10% of the time.

Vocalization analyses.—Frequencies of vocalizations and rates of duet singing were based on tallies of all vocalizations heard during scheduled observations in 2002, the year in which the most observation hours were completed (Table 1). To characterize the structures of male calls, vocalizations were recorded with a Sony TC-D5ProII Professional tape recorder and a Sennheiser ME66 shotgun microphone. Mechanical wing sounds were isolated from video recordings made with a Sony Hi-8 Handycam (CCD-TRV66 NTSC). Vocalizations were analyzed in SIGNAL, version 3.1

(Engineering Design, Belmont, Massachusetts), and RAVEN, version 1.2 (Charif et al. 2004.).

Statistical procedures.—Statistical analyses were conducted in JMP 5.0 (SAS Institute, Cary, North Carolina). I used parametric statistics when variables were normally distributed (Shapiro-Wilk test) and substituted nonparametric equivalents when they were not. Results are presented as means \pm SD.

RESULTS

Characterization of display areas.—The density of display areas on the study site was \sim 1 per 1.1 ha of uncleared land. Display areas were irregularly shaped, were spaced 102 ± 30 m apart, and averaged $2,480 \pm 1,060$ m² in area (range: 525–4,500 m²; $n = 24$ display areas). All display areas included in this study were in auditory but not visual contact with at least one neighboring display area.

Display perches were live horizontal saplings or vines on which the males performed dance displays. These display perches were usually arched and averaged 62 ± 24 cm high at the highest point ($n = 13$) and 1.2 ± 0.2 cm in diameter ($n = 12$). Display areas included one to four display perches used by the same pair of males (mean = 2.2 ± 0.9 perches, $n = 26$ display areas). When one display area included multiple display perches, they were 40.4 ± 26.7 m apart (range: 11–107 m; $n = 45$ interperch distances in 19 display areas, total = 49 display perches). Displays in a given display area usually occurred on one perch, though courtship of an individual female sometimes involved sequential displays by the same males on several perches.

Both display areas and display perches were reused in multiple years and remained in use even when the birds attending them changed. Saplings apparently appropriate for use as dance perches were ubiquitous on the study site, and the destruction of one display perch resulted in males displaying on another display perch within their display area ($n = 3$ perch replacements).

Display-perch maintenance behavior.—Males regularly “cleaned” the area around the display perch by tearing pieces from nearby leaves, usually by hovering to peck at the vegetation. When a leaf piece was torn off, the male returned to the perch before dropping it. Males also pecked at the display perch itself, and display perches

had a characteristic pattern of scratch-like marks apparently produced by this behavior. Scratches marked 61.5 ± 12.6 cm of the perch ($n = 10$ perches), approximately the length normally used during dance displays. Males never cleaned display perches when females were present.

Daily activity patterns.—During the breeding season, male Lance-tailed Manakins were present and active on their display areas throughout the day. Duet singing and dance displays for females were observed during all daylight hours, with a relatively inactive period in the mid-morning (Fig. 2A, B). Copulations, too, took place throughout the day, but were somewhat more common in the early afternoon than at other times (Fig. 2C).

Seasonal activity patterns.—Breeding activity, consisting of dance displays for females, copulations, and nest initiations, consistently started in March and peaked in April and early May. The earliest nests found each year were initiated between 1 and 24 March ($n = 4$ years). Nesting continued through early June, and nest initiations were observed on the site as late as July 1. From March until mid-June, >50% of females captured in mist nets had brood patches (Fig. 3). There was a general decrease in the rate of courtship displays performed for females from late March to early July (linear regression of display rate on week of the year: 2002: $R^2 = 0.31$, $F = 6.26$, $df = 1$ and 15 , $P = 0.03$; 2003: $R^2 = 0.62$, $F = 11.45$, $df = 1$ and 8 , $P = 0.01$). No significant trend was detected in 2001 ($R^2 = 0.05$, $F = 0.70$, $df = 1$ and 15 , $P = 0.41$); observations in 2004 spanned an insufficient period to examine this pattern. Observations during November 2001 revealed that the same males observed during the breeding season were present and singing on their display areas at this time, though they were less active than in March–June. Three dance displays for females were recorded in November, but none ended in copulation.

VOCALIZATIONS AND MECHANICAL SOUNDS

Males vocalized regularly while on their display areas, whether or not other birds were present. Lance-tailed Manakins had a repertoire of seven common and two less-frequent individual calls (Table 2; Fig. 4). In addition to vocalizations by lone individuals, the vocal repertoire of male Lance-tailed Manakins included

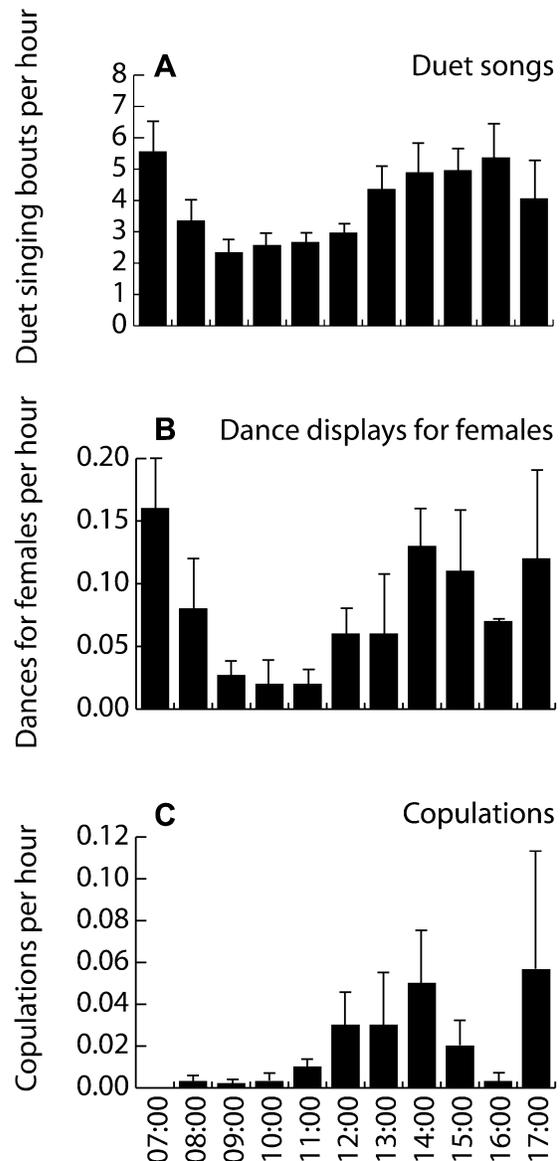


FIG. 2. Occurrence of male displays by time of day. Mean numbers of (A) duet singing bouts, (B) dances for females, and (C) dances ending in copulation initiated per hour of observation. Error bars indicate one standard error of the mean. Analyses were limited to observation sessions at display areas observed two or more times per week in each field season. Total observation effort at these areas was 970 h in 2001, 1,641 h in 2002, 423 h in 2003, and 157 h in 2004. This represents 9,910 duet song bouts, 203 displays for females, and 35 copulations in four years.

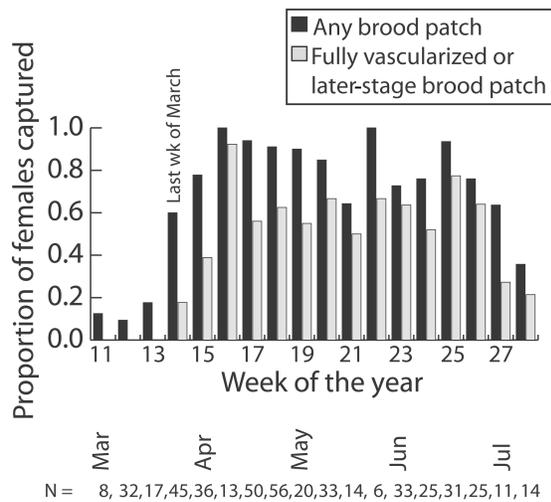


FIG. 3. Seasonality of breeding in the Lance-tailed Manakin. Captures of females with brood patches indicate that nesting begins in late March and continues through early July. This analysis includes all captures from 1999 to 2004, when at least five females were captured in the same week of the year ($n = 469$ captures). The development of a brood patch corresponds with individual breeding state in female Lance-tailed Manakins. Females in early stages of breeding exhibit defeathering or slight vascularization of the breast area, whereas females that have laid eggs have brood patches that are fully vascularized and swollen, a condition that subsides as nesting is completed.

coordinated calls by multiple individuals, which occurred in several different contexts.

Duet singing.—The most common and complex cooperative vocalization was the duet song. Duetting pairs of males perched ~10 cm apart on a high branch and repeated a synchronized call phonetically resembling the phrase “querico” (kay-REE-ko). These calls were generally similar to the “toledo” calls of Long-tailed Manakins (Slud 1957, Foster 1977, McDonald 1989b), but they were “scratchier,” had a slightly shorter second syllable, and were regularly interspersed with high up-whistle notes (called “salir” here to distinguish them from solitary up-whistles described in Table 2), which were not reported in Long-tailed Manakin duets. Duet songs were often sung in groups of three *querico* elements, repeated with a slight pause (~2 s) between repetitions: *querico salir-querico querico* (Fig. 4H). The average rate of *querico* calling was $14.6 \pm$

6.2 *quericos* per minute of duet singing ($n = 2,736$ bouts ≥ 30 s long), with the *salirs* occurring at a rate of 4.2 ± 2.9 min^{-1} of duetting.

The *querico* portion of duet calls had a low frequency range (1.3–1.5 kHz), whereas the *salirs* spanned 2.0–2.5 kHz in an ascending whistle (Fig. 4H). Typically, only one bird gave the *salir* at a time, though this role was sometimes traded between partners several times within a bout of duet singing. The male that gave the *salir* call threw his head downward and visibly expanded his throat as he called, presumably through inflation of an air sac. Sonograms confirmed that the *saliring* male gave a *querico* call immediately after this whistle element, whereas his partner usually gave only the *querico* call (Fig. 4H). Either male of a duetting pair sang the first note of the duet; the identity of the individual initiating the duet often changed over the course of a duetting bout. Females were not directly in attendance during duet song bouts. However, duet songs were loud and were usually performed from high perches, making them easily heard from some distance.

Querico calls were also given by individual males in the absence of a partner, though this was a rare occurrence (Fig. 4J). When these solo *querico* bouts occurred, they generally lasted for no more than a few seconds, with one to four repetitions of the *querico* call. Of 137 solo *querico* bouts recorded in 2002, 107 (78%) lasted for <10 s. Longer (2–3 min) bouts of solo *quericos* were observed but occurred even more rarely (2% of 265 solo bouts in 2002).

Querico-graaw.—Some bouts of duet singing included a low, growl-like “graaw” component (8.8% of duet song bouts; $n = 11,045$ total duet bouts observed in four years). In these bouts, the *querico* calls were regularly punctuated by a *graaw* call given as the calling male darted rapidly from the *querico* perch to a similar high perch 0.5–1 m away. This did not interrupt the rhythm of *querico* calls, but rather filled the pause normally heard between *quericos*. One or both males performed a *querico-graaw* during a song bout. When both males gave this call, they did so alternately and performed the *graaw* display between *querico* vocalizations. No *salir* calls were given during the portions of duet singing bouts in which males performed the *querico-graaw* display ($n = 979$ *querico* bouts with *graaw* display, 2001–2004).

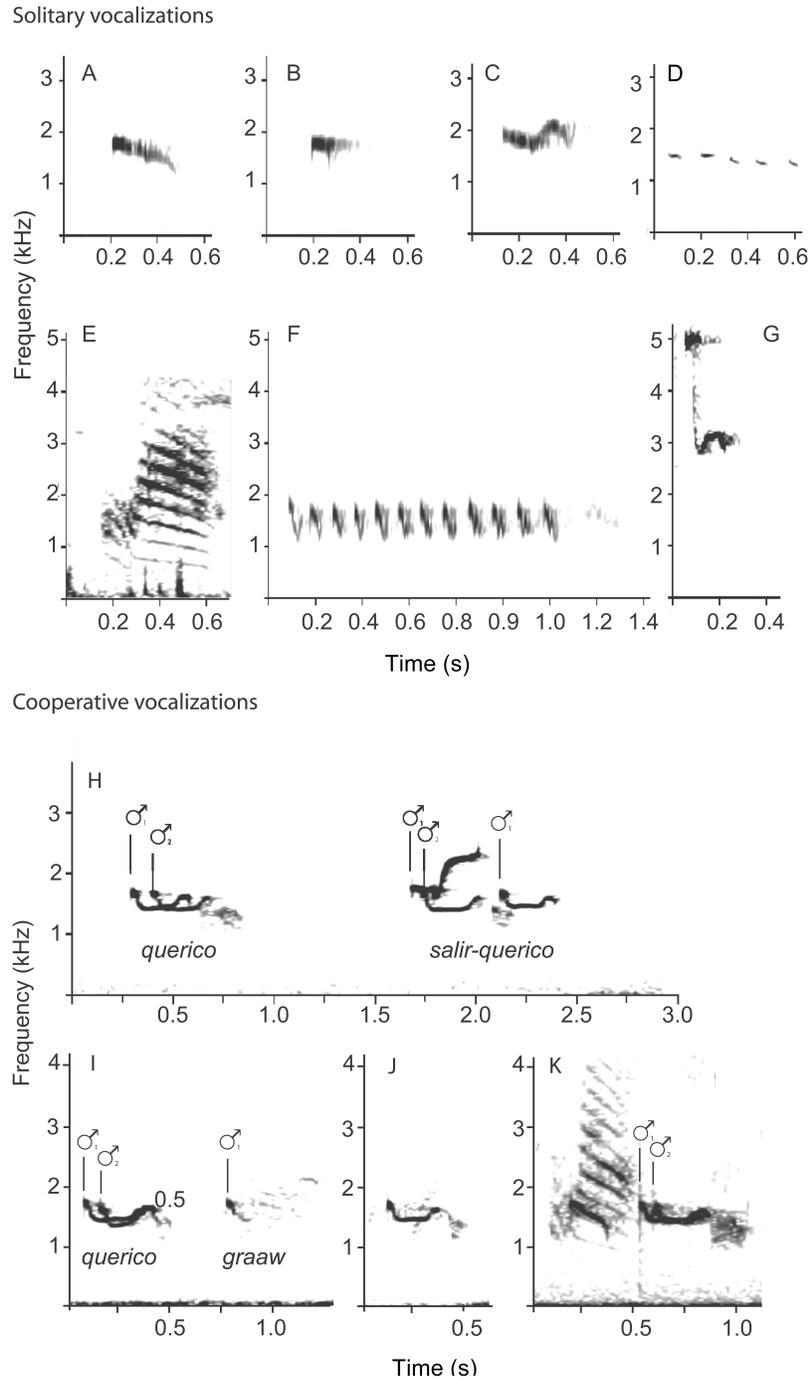
Dance call.—This was a twangy “nraawnraawn-raaw” call given by males as they performed

TABLE 2. Individual Lance-tailed Manakin vocalizations and the rates at display areas in 2002.

Vocalization Description	Number of calls per hour (mean ± SD)	Identity of caller	General context
<i>Down-whistle</i> Whistle descending from 2 to 1.25 kHz and lasting ~0.3 s.	110.29 ± 36.62	Males and females	Contact call, alarm call, courtship elicitation by females
<i>Pip</i> A high (2 kHz), short (0.2 s) note with a constant pitch frequently given in series, with 2–5 s between <i>pips</i> .	52.53 ± 20.88	Males only; usually territorial males	Courtship, casual
<i>Trill</i> A 1–2 s series of descending notes repeated in quick succession, creating a warbling effect.	27.06 ± 13.17	Males only	Loafing
<i>Wah</i> A throaty call phonetically resembling its name that has a broad frequency range, generally 1–3 kHz, and lasts ~0.4 s. Often interspersed into duet songs (Fig. 4K).	49.97 ± 21.17	Males only	Short-range interactions among males
<i>Up-whistle</i> A piercing, two-syllable vocalization that starts at 2.0 kHz and rises to ~2.2 kHz.	16.02 ± 12.48	Males only	Casual
<i>Beg</i> A high-pitched call directed at another individual in proximity. Usually given by the displaced individual in fights or displacement interactions.	0.56 ± 0.44	All	Fights—subordination
<i>Eek</i> A sharp, metallic call given at the end of a bout of leapfrog dancing. Only one male <i>eeked</i> in dances for females, but males often <i>eeked</i> simultaneously or in quick succession when no female was present.	– ^a	Males only	During dance displays
<i>Chatter</i> A soft, quickly repeated, constant tone heard when females mobbed researchers near nests.	Rare	Females only	Extreme agitation; while mobbing
<i>Squawk</i> A loud, dissonant call likened by some observers to a pig's squeal. Not during dance or song displays.	Rare	Unclear	Unclear

Total vocalizations heard at each display area in 2002 were summed and divided by the number of observation hours at that area. Analysis was limited to display areas observed for >25 h. *n* = 25 display areas averaging 50.76 ± 24.19 observation hours each (1,269 total hours of observation). Vocalizations were usually given by multiple individuals in the area, and so rates represent general activity in one display area rather than the calling effort of individual manakins. “Casual” indicates situations when calls are regularly given with no clear recipient or event context. Sonograms of the seven most common calls are given in Figure 4.

^aNot tallied independently of displays.



either “up-and-down” or “leapfrog” jumps on the dance perch (see below). Males leaped alternately and called as they leaped, producing a continuous, rhythmic call. Males that performed leaping displays in the absence of other males or females still gave the *nraaw* call with every leap.

Sonations.—Mechanical sounds or sonations are intentionally modulated sounds produced by structures other than the syrinx and used for the purpose of communication (Prum 1998, Bostwick and Prum 2003). Two sounds produced during Lance-tailed Manakin courtship displays were apparently mechanical in origin.

Wing-clicks.—These were short pulses of noise produced during slow flight displays (see below). Clicks were 0.12–0.2 s apart and spanned the full range of standard sonogram detection, from <1 kHz to 12.5 kHz (Fig. 5). Approximately 7–30 clicks were repeated in quick succession, sounding similar to the echolocation clicks of a bat as heard through a bat detector. This mechanical noise was more common in displays for females (8.9% of 216 total displays observed in four years) than in displays when no females were present (1.0% of 1,457 displays observed in four years). Speed and loudness of clicks varied within individual displays.

Woosh.—This was a low-frequency sound, <1 s in duration, heard at the low point of some swoop and quick-down displays (see below). No sonogram is available. Prum (1998) reported that all manakin species that produce mechanical sounds have dimorphic flight-feather specializations. Consistent with this observation, the distal primaries of definitive male *C. lanceolata* appeared to have slightly stiffer rachi than those of females. The tips of the first three primaries are also emarginated on their leading edges.

DISPLAYS FOR FEMALES

The display repertoire of the Lance-tailed Manakin included both solo and paired male displays (Fig. 6). Dance displays performed for females involved a series of ≤ 11 unique display elements that are presented here in the order in which they typically occurred in a complete display (Fig. 7). Dance displays for females were performed almost exclusively by males in definitive plumage (99.1% of 228 displays). When a definitive-plumage male twice performed courtship displays with a partner in predefinitive

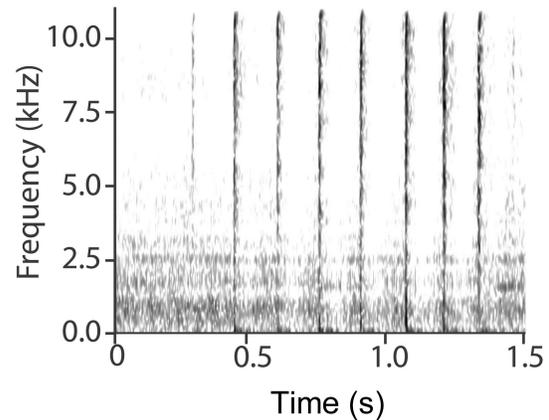


FIG. 5. Mechanical wing-click sound heard during some slow-flight displays. Frequency range of wing clicks almost certainly extends past the Nyquist frequency of 11.025 kHz, but the sampling rate (22.050 kHz) precludes representation of higher frequencies. Sound was band passed in RAVEN, version 1.2.1 beta, before sonogram was generated to prevent aliasing.

plumage, the female remained on the display perch for <30 s and did not copulate.

Pip flight.—During this flight display, one or two males broadly circled the display perch area, landed on high perches 6–10 m apart, and gave a “pip” call each time they landed. When two males were present, the pip call of one male was followed immediately by a down-whistle from the other. Displaying males were at times separated by ≤ 7 m, but at other times they landed side-by-side on the same branch. If a female approached or down-whistled in response to these calls, the males gradually approached and eventually landed on the display perch, flicking their wings. If only one male was present, the male continued pip flight or began solo slow-flight (described below). If two males were present, they continued pip flight or began two-male slow-flight, up-and-down, or leapfrog dance displays.

Paired slow flight.—The two displaying males flew with slow, labored wing beats in an area 5–10 m around the display perch. Males crossed flight paths or followed each other from perch to perch, often simultaneously giving pip or coordinated pip-down-whistle vocalizations when they landed. Males frequently landed on the display perch and remained on any given perch for no more than a few seconds, flicking

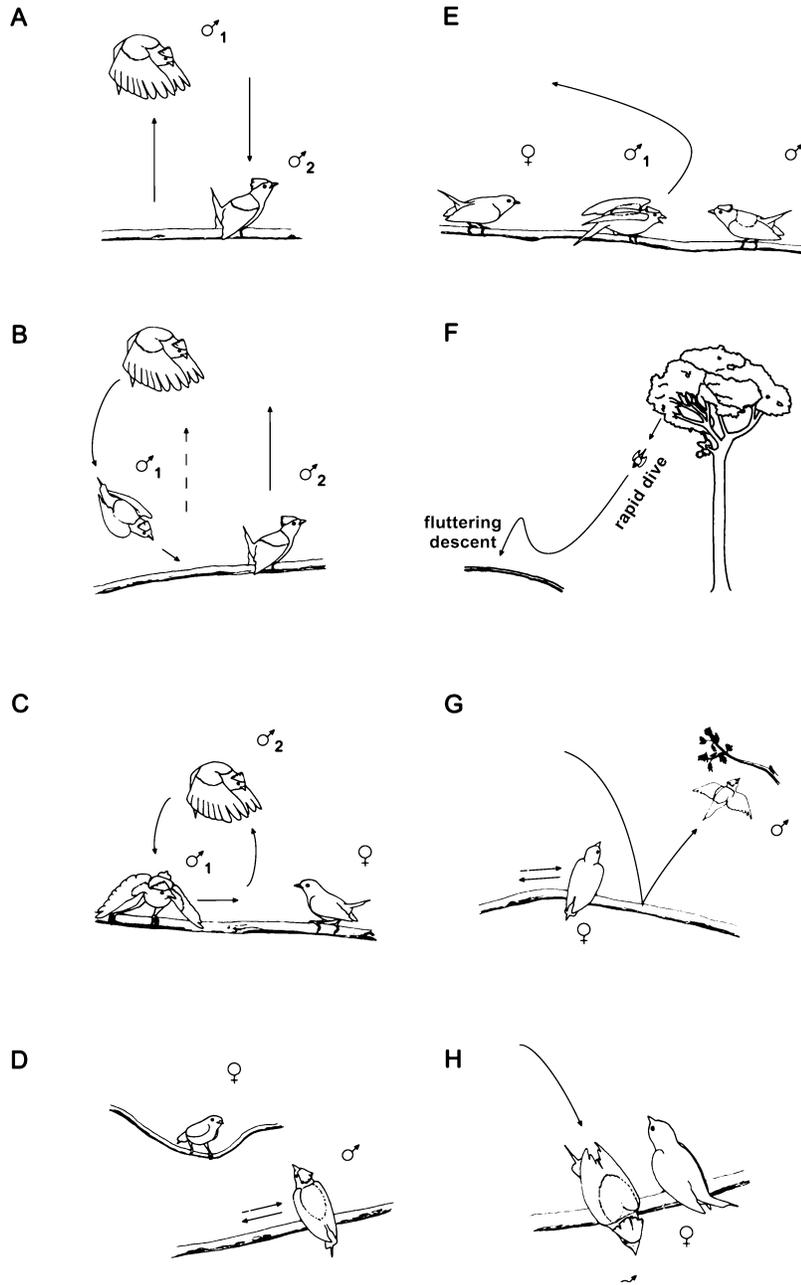


FIG. 6. Lance-tailed Manakin dance displays: (A) up-and-down display; (B) quick-down variant of the up-and-down display; (C) leapfrog dance; (D) back-and-forth by male after female leaves the display perch, (E) *eek* display following a bout of leapfrog dancing. The alpha (male 1) gives the *eek* vocalization and leaves the display perch before his partner follows; (F) swoop; (G) bounce at the end of a courtship sequence, with back-and-forth by the female; (H) bow before copulation.

their wings and wiping their bills on the branch. The paired slow flight was always performed between bouts of leapfrog dancing and usually preceded these dance displays (Fig. 7). Similar displays have been termed "butterfly flight" in

Long-tailed Manakins (Slud 1957, McDonald 1989b); this designation is not used here because it has also been used for flight displays characterized by postures and motions distinct from those observed in Lance-tailed Manakins, such

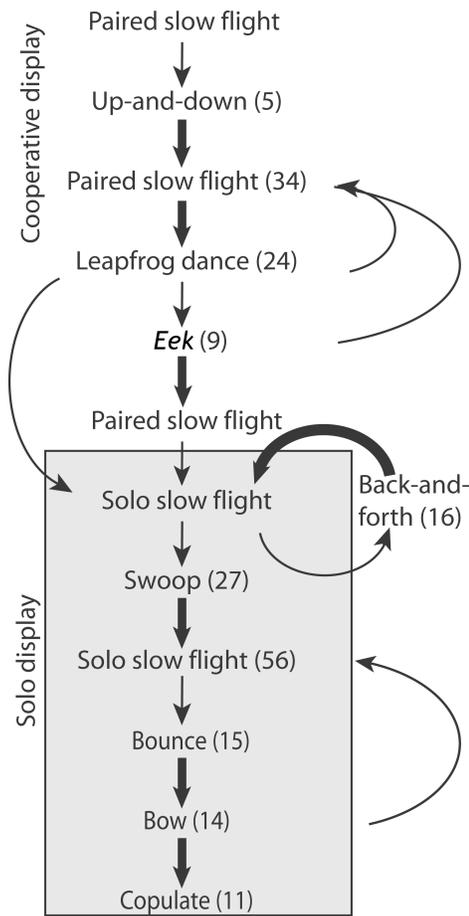


FIG. 7. Schematic diagram of the courtship display sequence. A complete courtship display is a variable combination of display elements and may include repetition of several elements in predictable combinations. Here, arrows link display elements that followed the preceding display in $\geq 10\%$ of occurrences during displays for females. Thick arrows represent transitions in which the subsequent display followed the initial one in $>50\%$ of occurrences. $n = 200$ display element transitions in 16 displays ending with copulations or copulation attempts. Sample sizes for the number of repetitions of individual display elements are given in parentheses. Curved arrows represent repetition or deletion of intervening display elements. Fifteen of the displays involved two males, and one involved only one male. One-male displays included the same elements as two-male displays that had progressed to the solo display phase (indicated by the shaded box). Both two- and one-male displays were often preceded by *pip* flights, which are not shown here.

as shallow wing beats in Band-tailed Manakins (*Pipra fasciicauda*; Robbins 1983) and vertical body posture in White-bibbed Manakins (*Corapipo leucorrhoa*; Rosselli et al. 2002).

Up-and-down.—Two males alighted on the display perch ~ 5 cm apart and leaped alternately into the air. The males hovered briefly over their place on the display perch and landed in this same location (Fig. 6A). As they leaped, each male gave the dance-call vocalization. Males elevated their beaks while on the display perch and frequently flicked their wings excitedly. As males hovered, they lower their heads in relation to their bodies and flared their red crests.

Up-and-down displays occurred in 27.3% of courtship displays for females ($n = 216$ displays). Females were usually present but not positioned on the display perch during up-and-down displays. Instead, this display seemed to draw the female to the display perch, and ended when she alighted beside the males. At this time, males either performed an immediate leapfrog dance display, or a brief paired slow flight followed by leapfrog dance display (see below). In a slight variant of the up-and-down display, males sometimes added a quick-down swoop to their descent, in which they returned to the display perch in a slight downward arch and descended more rapidly than during the usual hovering action (5.1% of 216 displays for females; Fig. 6B). This quick-down variant was accompanied by a somewhat more staccato dance call than was heard in other up-and-down displays.

Leapfrog dance.—With the female perched on the display perch, the male closest to the female (male 1) leaped into the air and hovered as in the up-and-down display. As the hovering male descended to the display perch, he landed slightly behind his departure point. While male 1 was in the air, male 2 ducked his head and hopped along the display perch into the departure place of male 1. As male 1 landed, male 2 leaped into the air and hovered in the same manner (Fig. 6C). As each male leaped, he gave a dance call. As in the up-and-down display, males extended their crests as they hovered. Males hovered within 5 cm of the female but never came into physical contact with her. The female often remained motionless on the branch during this display, though in some instances she flicked her wings, took small hops toward the dancing males, and ducked her head as each

male leaped. With each leap, the male turned to face the female and hovered directly in front of and slightly above her. If the female turned on the branch, the males adjusted their orientation to continue hovering directly in front of her.

The leapfrog dance usually continued for 10–45 s at a time; males then broke off to perform a paired slow flight around the display perch while the female remained on or near the perch. Males returned to resume leapfrog dancing after 3–10 s. If the female left the display perch during a leapfrog dance, males immediately began a slow flight around the perch. Some bouts of leapfrog dancing ended with an “*eek*” display (see below).

Back-and-forth.—One male crouched with his crest flared and beak uplifted and darted rapidly back and forth on ~10 cm of the display perch (Fig. 6D). Frame-by-frame video analysis of this display showed that males moved with rapid, single leaps along the horizontal axis of the display perch, sometimes propelling themselves with a downward flap of one wing. This movement was unlike the multiple short hops in the “slide” displays of *Pipra* spp. (Sick 1967), but it was similar to a rapidly repeated performance of the “lateral spring” of Club-winged Manakins (*Machaeropterus deliciosus*; Bostwick 2000). Back-and-forth was usually performed when a female was positioned in nearby vegetation and occurred in 25.9% of displays for females ($n = 216$ displays). Following this display, the female flew to the dance perch, displacing the displaying male as she landed. Females sometimes did back-and-forth displays during male slow flights, usually after several minutes of courtship (26.8% of 216 displays for females).

Eek display.—Immediately preceding the *eek* display, the leapfrog display behavior became increasingly frenzied, with lower leaps and faster repetition of the dance call. Instead of leaping into the air during the final moments of this dance, one male turned to face the other, placing himself between the female and his dance partner. He then gave an *eek* call (see above section on vocalizations) and forcefully leaped in an arc off the dance perch (Fig. 6E). After a brief pause, the second male also left the display perch without vocalizing. Males then (1) continued slow-flight displays and returned for another bout of leapfrog dancing or (2) ceased dual-male display (Fig. 7). If dual-male display

ceased, the second male left the immediate vicinity of the display perch while the male that gave the *eek* call returned to continue solo displays for the female. The *eek* and departure of the second male usually occurred after leapfrog displays late in the display sequence (Fig. 7).

Solo slow flight.—One male flew around the dance perch in the same slow, labored pattern as during the paired slow flight. This display usually followed several minutes of dual-male display and always preceded copulation (100% of 39 copulations). The displaying male frequently performed sloop, back-and-forth, or bounce movements (see below) during this solo slow flight. The female usually perched on the display perch during this display.

Quick-turn.—This was a 180° turn executed in a stereotyped manner during some slow-flight displays. The turning male paused briefly as he landed at the end of the slow flight trajectory, then rapidly reversed direction, usually moving 6–12 inches from his starting point on the perch as he turned. After another brief pause, he continued slow-flight displays.

Swoop.—To initiate this display, one male flew to a high branch, 10–20 m away from the display perch and in the lower part of the canopy. As he landed on this high perch, he gave a single *pip* call. After a brief pause, he returned in an extremely rapid dive to the display perch, arcing downward and braking his descent with an upward swoop directly over the perch. He then fluttered down and landed on or near the display perch before resuming the slow-flight display (24.1% of 216 displays for females; Fig. 6F). An associated *woosh* noise was sometimes heard at the nadir of the swoop (described above). This swoop display occurred during paired or solo slow-flight displays.

Bounce.—The displaying male flew from a nearby twig to the display perch, descending vertically and touching the display perch only briefly before flying back to a twig near his original position, so that he appeared to bounce off the display perch (Fig. 6G). This movement was observed at the end of a courtship display immediately before a copulation attempt and was usually repeated two to three times in quick succession. Bounces never occurred when more than one male was displaying.

Bow.—After performing the bounce display, the male landed on the display perch beside the female but faced the opposite direction.

He paused with his head below the level of the display perch and his red crest feathers fully spread and maintained this pose for 1–2 s before attempting copulation (Fig. 6H). This display was never observed without preceding bounce displays or a subsequent copulation attempt. Blue-backed Manakins perform a similar bow, but from a branch facing the female, then land facing in the same direction as the female before mounting her (Snow 1963). In the Lance-tailed Manakin, the bow was invariably performed on the display perch, but the male faced the opposite direction from the female and turned in the air to mount.

Copulation.—After the bow, the male leaped into the air, reversed direction, and landed on the female's back to copulate. Only males in definitive plumage were observed copulating. In most cases (95% of 39 copulations), the male copulated once and then left the display area. After the male departed, the female straightened her legs and lowered her tail, then remained on the dance perch for ≤ 1 min while preening.

All observed copulations ($n = 39$ copulations) occurred on the display perch after ≥ 30 s of solo male display. Fifty percent of displays that ended in copulation did not include any paired male displays ($n = 17$ of 34 displays observed from start to finish). Solo displays included the same elements as the solo portions of two-male displays: solo slow-flight, back-and-forth, swoop, bounce, and bow. Multiple copulations with the same female during one display sequence occurred rarely ($n = 2$ displays by different males, 2 and 8 copulations each).

Female behavior during courtship displays.—Females were active participants in courtship displays. Individual females exhibited a range of behavior during courtship, from preening and regurgitating seeds to actively following males' movements with head motions or short flights off the display perch. Attentive females ducked their heads and took little hops toward males engaged in leapfrog displays, executed back-and-forth displays during male slow-flights (sometimes propelling themselves with exaggerated downbeats of the outside wing), turned sharply to watch males as they passed the display perch, and occasionally left the display perch to follow males during slow-flight displays. As described in Long-tailed Manakins (McDonald 1989b), females that copulated did

so only after exhibiting at least some of these attentive behaviors ($n = 39$ displays ending in copulation). It was not uncommon, however, for females to behave in this manner and then leave before copulation. By contrast, female postures in the moments immediately preceding copulation seemed to reliably indicate willingness to mate: video analysis demonstrated that as the male performed the last in a series of bounce displays, receptive females lowered their wings and raised their tails slightly and lowered their bodies to a horizontal position.

DUAL-MALE DISPLAYS WITH NO FEMALE PRESENT

In addition to performing cooperative courtship displays for females, males also performed paired displays when females were not present. Males of any plumage class participated in these displays. These displays contained elements resembling those in displays performed for females, but males displaying with no female present usually directed their movements toward their male partner, rather than toward a third bird or the position in which a third bird would be if present.

A variant of the up-and-down display, the fly-at display (*sensu* Foster 1981), occurred only when no females were present. As in the up-and-down display, males leaped alternately and hovered above the display perch, but in the fly-at display, each hovering male faced his partner and advanced slightly toward the male while in the air, then retreated to land where he started. Leapfrog dance displays performed in the absence of females usually lacked the clockwork regularity of leaps done in the female's presence and often included only one or two leaps. When no female was present, one or both displaying males gave the *EEK* call at the end of leapfrog, fly-at, or up-and-down displays. When two males *EEKED*, they called either simultaneously or with calls offset by a few seconds.

Males also performed dance display elements with no other conspecifics present. Males performing alone could be of any plumage class. These males frequently repeated the same one to three display elements more times than observed in displays for females and interspersed their display with maintenance activities like cleaning the display perch or preening.

DISCUSSION

The spatial arrangement of Lance-tailed Manakin display areas is consistent with an exploded or dispersed lek mating system (Bradbury 1981, Prum 1994). The definition of the lek in the genus *Chiroxiphia* has been complicated by the fact that groups of males aggregate within display areas (Foster 1977, 1981; McDonald 1989a; Trainer and McDonald 1993). Leks of *Chiroxiphia* have been defined as either (1) a group of display perches on which one pair of males displays for females (Prum 1994; Long-tailed Manakin, McDonald 1989a; Swallow-tailed Manakin, Foster 1981) or (2) the larger aggregation of multiple pairs of displaying males assessed by females as they select mates (Long-tailed Manakin, Foster 1977). In the Lance-tailed Manakin, only one male at each display area performs the solo displays that always precede copulation (DuVal 2007). Therefore, each display area is effectively the territory of one male with which a female could mate, and the lek is most appropriately defined as the aggregation of display areas that a female may visit to select a mate. Because all display areas were within earshot of at least one other display area, all are considered to be part of one dispersed lek.

The complex behavioral repertoire of the Lance-tailed Manakin includes 11 courtship display elements and 7 common vocalizations, as well as two sonations never before reported in this genus. As is typical for *Chiroxiphia*, pairs of male Lance-tailed Manakins perform duet songs and dance displays. However, comparison with published sonograms shows that the song elements vary notably among species of *Chiroxiphia* (Blue-backed Manakin, Snow 1963; Long-tailed Manakin, Trainer et al. 2002). Duet song is not a regular part of Swallow-tailed Manakin behavior (M. Foster pers. comm.). Lance-tailed Manakin duets are most similar to those of Long-tailed Manakins, but they are comparatively variable because of the occurrence of regularly interspersed up-whistle notes. The coordination of solitary calls frequently occurs before duet songs and may serve to synchronize singing males but does not seem to be part of the duet itself, because these calls are not included in many duet songs (Fig. 4K). This is contrary to a study by Pacheco and Laverde (2002), who included a coordinated

“wah” and down-whistle in the description of a cooperative duet.

The dance call of Lance-tailed Manakins is also similar to that of Long-tailed Manakins, but in Long-tailed Manakins, the basic *nraawn-raawnraaw* call is overlaid with a sharp “miaow-raow” call, which is the dominant sound in dance displays for this species (Slud 1957, E. H. DuVal pers. obs.). The dance repertoire of all species of *Chiroxiphia* includes alternating up-and-down leaps, a backwards leapfrog or “cartwheel” display, solo and paired slow flight or “butterfly” displays, and some variant of the *eek* call (Swallow-tailed Manakin, Foster 1981; Blue-backed Manakin, Gilliard 1959, Snow 1963; Long-tailed Manakin, Slud 1957, Foster 1977). *Pip* flight and bounce displays have not been explicitly described for other species of *Chiroxiphia*, but comprehensive descriptions of all courtship display elements are not available, and so it is unclear which of the many display elements of Lance-tailed Manakins are unique to this species.

Dance displays were frequently performed with no females present and even occurred without other males present. Multimale displays in the absence of females may function in establishing dominance at each display area or serve in the development of display skills. The observation of completely solitary displays suggests that practicing display elements even without direct social stimuli may be important for the development of display skills in this species. Further study is needed to test the possibility that individual males improve their performance of the complex, physically demanding courtship displays by this solitary repetition of display elements.

Timing of breeding activity.—Male Lance-tailed Manakins remained on display territories and actively displayed throughout the day. Lek activity and visits by females seemed less influenced by time of day than has been reported for several manakin species (e.g., White-bearded Manakin [*Manacus manacus*], Shorey 2002; Club-winged Manakin, Bostwick 2000), though other species also remain active during all daylight hours (e.g., White-bibbed Manakin; Rosselli et al. 2002). The March–July breeding season reported here is roughly consistent with previous data indicating that Lance-tailed Manakins breed in May and June in northeastern Venezuela (Friedmann and

Smith 1955). Courtship probably continues into August and September, given records of nesting females found incubating on 11 August and 13 September in the Panama Canal zone (Hallinan 1924). Males seem to remain on their territories year-round and maintain display associations with their breeding-season display partners during the apparent nonbreeding season.

The extended breeding season and long daily periods of lek attendance described here suggest that females have multiple opportunities to assess males. Indeed, females may observe male displays year-round, as suggested by observations of females attending dance displays in November. These visits, as well as courtship during the peak breeding season, may influence subsequent mate-choice decisions. The extended period of male-male affiliation also has implications for the development of cooperative coalitions among males. Long-term association of male partners may facilitate the formation of stable dominance relationships or the development of tightly coordinated displays between partners.

Sonations.—Although the production of intentionally modulated mechanical sounds has been well documented in other Pipridae (Snow 1963, Sick 1967, Prum 1998, Bostwick 2000), these are little-known in the genus *Chiroxiphia*. This study confirms the existence of mechanical sounds in *Chiroxiphia*. Lance-tailed Manakin wing-clicks are of low amplitude and consist of many consecutive clicks, unlike the wing sonations produced by manakins in the genera *Corapipo*, *Ilicura*, *Manacus*, and *Pipra* (Prum 1998). Wing-clicks are most likely produced by rachi hitting other rachi of the same wing during flight. The low-frequency “woosh” sounds of Lance-tailed Manakins seem similar to the short, low-frequency sound pulses produced by *Pipra* spp. and *Corapipo* spp., which are also produced at the nadir of a flight display and are probably caused by the compression of air with the wings at high speed (Prum 1998, Bostwick and Prum 2003). Mechanical sounds and sexual dimorphism in the structure of the primaries have been previously reported in this genus (Gilliard 1959, Snow 1963) but were neglected in the existing phylogenetic analysis of manakin mechanical sounds (Prum 1998). Interestingly, the sounds produced by Lance-tailed Manakins differ from those of Blue-backed Manakins, in which males produce a single click upon takeoff for a swoop

display. The presence of mechanical sounds in *Chiroxiphia* is evolutionarily significant, in that it suggests either an additional independent origin of sonations in Pipridae, or that the node for the evolution of sonations lies before the divergence of *Chiroxiphia* spp. and other sonating species (Prum 1998). Furthermore, this implies additional losses of mechanical sound in some species of *Chiroxiphia* and *Antilophia*, unless further field research reveals mechanical sounds in these taxa or the phylogeny is revised.

Several characteristics of Lance-tailed Manakin mechanical sounds suggest that similar sonations may have been overlooked in closely related species. The wing-click and *woosh* sounds are low in amplitude and occur in only a small proportion of displays for females and almost exclusively when females are present. Furthermore, the structural modifications that may contribute to the production of these sounds are slight and easily overlooked with birds in the hand or when examining museum specimens.

Cooperative courtship behavior.—The cooperative duet vocalizations of Lance-tailed Manakins (1) consist of tightly synchronized calls, (2) require the participation of two males for the completion of the vocalization, and (3) are rarely performed by solitary individuals. Both the duet song and vocalizations given during two-male *pip* flights meet the definition of a duet—joint acoustic displays where two birds perform temporally coordinated songs (Farabaugh 1982, Hall 2004). The exact function of the duet song remains to be determined, though possibilities include advertisement of display-perch location for females, advertisement of male presence to males on neighboring display areas, or development and maintenance of coordination and pair bonding within the male pair itself.

The social relationships between males in display partnerships are discussed elsewhere (DuVal 2007), but individual dance displays performed by male pairs were highly cooperative. Males never attempted up-and-down or leapfrog displays for females unless a partner participated. These displays appeared to function directly in communication with potential mates at a display area, and only one male of a displaying pair performed the solo displays that always preceded copulation.

It is intriguing, however, that two-male displays did not always precede solo displays and copulations. In all three species of *Chiroxiphia*

studied to date, some copulations followed exclusively solo displays (Long-tailed Manakin, McDonald 1989a; Swallow-tailed Manakin, Foster 1981; Blue-backed Manakin, Snow 1963). In Swallow-tailed Manakins, these entirely solo displays represented a third of all displays for females (Foster 1981). I cannot exclude the possibility that females observing solo displays have previously observed the same males performing paired displays, but it is clear that females do not have to observe cooperative displays immediately prior to mating. Although some of the solo displays reported here may represent the conclusion of interrupted two-male displays, my observations included solo displays that ended in copulation after more than an hour in which no paired displays for females occurred. This plasticity in courtship behavior is a neglected feature of the behavioral repertoire of *Chiroxiphia* that draws renewed attention to the question of when and why males display cooperatively.

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