

DISPLAY BEHAVIORS, MECHANICAL SOUNDS, AND EVOLUTIONARY RELATIONSHIPS OF THE CLUB-WINGED MANAKIN (*MACHAEROPTERUS DELICIOSUS*)

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ABSTRACT.—Male Club-winged Manakins (*Machaeropterus deliciosus*) are known to produce a unique mechanical sound with their extremely modified secondary feathers, yet the species remains poorly known behaviorally. I observed lekking males in Reserva Maquipucuna, Pichincha Province, Ecuador, to better understand the role of mechanical sounds, the behavioral repertoire, and other details of the natural history of this species. The behavioral repertoire of *M. deliciosus* is much more diverse than previously documented; it includes four mechanical phrases, two vocal sounds, and seven display behaviors. Mechanical sounds constitute the most prominent elements of the species' displays, replacing vocal sounds for territorial advertisement. I examine possible homology of the observed behaviors and propose a new phylogenetic hypothesis, that *Machaeropterus* forms a monophyletic clade with the genus *Pipra*, based on the existence of a complex shared courtship display. Received 20 July 1998, accepted 1 October 1999.

THE FAMILY PIPRIDAE, the Neotropical manakins, is a clade of approximately 40 sexually dimorphic lek-breeding species (Prum 1992). The bright plumages and elaborate displays of male manakins have attracted considerable attention over the last century (e.g. Snow 1963b, Sick 1967, Prum 1990). Surprisingly, however, displays of most species in the family have not been observed or described in detail, and many are known by little more than anecdotal descriptions (Prum 1990, 1996).

The Club-winged Manakin (*Machaeropterus deliciosus*) is endemic to humid forests of the western slopes of the Andes in southwestern Colombia and northwestern Ecuador (Hellmayr 1929, Hilty and Brown 1990). Like most other manakins, they are sexually dimorphic. Females have drab olive-green plumage, and males have a chestnut-colored body, a red crown, and wings that are white ventrally but black dorsally with peculiar white, thickened shafts on the secondaries (Orejuela et al. 1982, Ridgely and Tudor 1994).

Darwin (1871) described the secondary feathers of male Club-winged Manakins as an example of structural modifications for production of "instrumental music," or mechanical sounds. Here, I use the term "mechanical sounds" to mean intentionally modulated

sounds produced by structures other than the syrinx and used for the purpose of communication (Prum 1998). The production of mechanical sounds, although common in manakins, is relatively rare in birds as a whole, and Club-winged Manakins produce mechanical sounds that are acoustically unique (Prum 1998). The lack of detailed behavioral information has hindered our understanding of the evolution and physical mechanics of this unusual mode of communication.

Although considered the best-known species in its genus (Prum 1990), current behavioral descriptions of Club-winged Manakins are incomplete. Willis (1966) and Orejuela et al. (1982) reported a display in which the wings are thrown open and mechanical sounds are produced. Willis (1966) noted that the wings produce the unusual mechanical sounds, but he did not observe the behavior in any detail. Indeed, the rapid and brief nature of the displays make them extremely difficult to describe without the aid of video. Orejuela et al. (1982) made extensive observations of habitat and lek characteristics and discussed the evolutionary importance of lek-breeding in this species. They also described the mechanical sound display in more detail, as well as a vocalization and copulatory behaviors. However, details necessary for understanding how the mechanical sounds are produced were lacking. Neither

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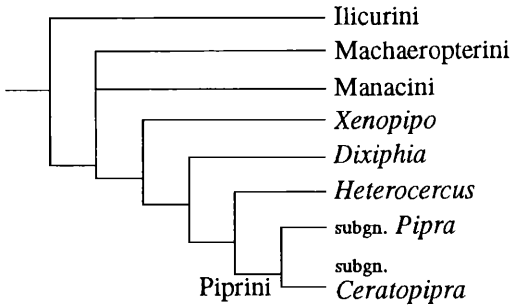


FIG. 1. Hypothesis of relationships among member taxa (tribes, genera, and subgenera) of Pipridae modified from Prum (1992). Tribe membership: Ilicurini includes *Ilicura militaris*, *Masius chrysopterus*, and *Corapipo* spp.; Machaeropterini includes *Machaeropterus deliciosus*, *M. regulus*, and *M. pyrocephalus*; Manacini includes *Lepidothrix* spp., *Manacus* spp., *Antilophia* spp., and *Chiroxiphia* spp.

the work of Willis (1966) nor Orejuela et al. (1982) attempted to describe completely the behavioral repertoire of Club-winged Manakins.

Analyses of the evolution of mechanical sounds have also been hampered by lack of knowledge of the closest relatives of the genus *Machaeropterus* within the Pipridae. Currently, two largely congruent hypotheses of phylogenetic relationships within the Pipridae have been published based on behavioral and morphological data sets (Prum 1990, 1992). The congruence between the behavioral and morphological phylogenies demonstrates the informative nature of behavioral characters in manakins (Prum 1990). The phylogenetic position of the genus *Machaeropterus* within the Pipridae was unresolved in both phylogenies (Prum 1990 and 1992; summarized and condensed in Fig. 1 to show the polychotomous and basal placement of *Machaeropterus*). Although Prum's 1990 behavioral data set is quite comprehensive (28 species, 44 characters), the display characterization of the Club-winged Manakin was based only on the observations of Willis (1966) and Orejuela et al. (1982) and thus was incomplete. Even less was known of the congeners (*M. regulus* and *M. pyrocephalus*), which were excluded from the behavioral analysis (Prum 1990). Similarly, the only structure used in the morphological analysis, the syrinx, is extremely reduced in all members of *Machaeropterus*, probably as a result of their extreme reliance on mechanical sounds for acoustic communication (Prum 1992). Thus, the unresolved and basal

placement of *Machaeropterus* may have resulted from a lack of informative characters. Many behaviors described herein for Club-winged Manakins have not been described previously and, therefore, may provide information on the relationships of this species to other manakins.

In this paper I have two objectives. First, I describe the display behaviors of male Club-winged Manakins, including detailed accounts of the displays, data on frequency of use of mechanical sounds, and other natural history observations. Second, I propose a new hypothesis of the phylogenetic relationships of the Club-winged Manakin suggested by the new behavioral information and discuss its implications for the evolution of mechanical sounds.

STUDY SITE AND METHODS

Behavioral description.—Orejuela et al. (1982) suggested that leks of Club-winged Manakins are active for at least eight months of the year, including October and November. I observed, tape-recorded, and video-taped male Club-winged Manakins for 82 h from 28 October to 27 November 1996 at a lek on the northeastern border of the Reserva Maquipucuna, Pichincha Province, northwestern Ecuador (00°08'N, 78°38'W, 1,500 m elevation). The lek is located 1.5 km northwest of the T. H. Davis Ecotourist Center in a strip of secondary forest (25 × 120 m) in a small ravine on a steep hillside. Except for a small (ca. 100 × 100 m) patch of primary forest, the ravine is separated from other forest by a grassy pasture with scattered trees.

Average daily minimum and maximum temperatures were 15°C and 24°C, respectively, and relative humidity ranged from 72 to 96% (\bar{x} = 92.1%). Local people regarded the study period as the beginning of the rainy season, but the region received unseasonably low precipitation (no rain in 19 of 29 days) during the period of my study.

I observed unmarked individuals using 8 × 40 binoculars. I made one all-day watch (0600 to 1630) to document the temporal pattern of activity. Thereafter, I conducted observations between 0600 and 1130 EST (although display activity always declined substantially by 0900). No blind was used, and all notes were taken by hand. Audio recordings were made with a Sony TCM 5000 recorder and Sennheiser ME 80 microphone. Video recordings were made with a Canon L2 8-mm camcorder using a 15× lens and a 2× teleconverter. Shutter speeds of 1/60 to 1/1000 s were used as permitted by lighting conditions to capture the motions of the displaying birds as clearly as possible. Individual identities and territorial boundaries were inferred from behavior when possible.

I measured several characteristics of the most frequently used mechanical sound display (the wing-flash display), which is usually composed acoustically of two *ticks* followed by one *ting*. Frequencies of *ticks* preceding *tings* were counted from 200 videotaped wing-flash displays. For two males, I measured the following parameters from sonograms of 20 wing-flash displays produced using CANARY 1.2.1 (Charif et al. 1995): (1) the time interval between the onsets of the first and second *ticks*, (2) the time between the onset of the second *tick* and the initiation of the *ting*, (3) the duration of the *ting*, (4) the fundamental frequency (lowest frequency tone in a set of harmonically related tones) of the *ting*, and (5) the frequencies of the first three harmonics.

Three displays (wing-flash, backward wing-flash, and crouch-call; see below) contain prominent acoustic elements that allow detection of their use without direct visual observation. To estimate relative frequencies, I counted the numbers of each display heard from the lek (i.e. all audible males at once) in one sample of each of the 18 10-min intervals between 0630 and 0930. The representative sample for each 10-min interval was selected randomly from days between 29 October and 25 November 1996 that had observations for the appropriate time interval available.

Phylogenetic analysis.—I examined the characters delineated in the behavioral data matrix of Prum (1990) for behaviors that are potentially homologous with those I observed in Club-winged Manakins. I scored Club-winged Manakin behaviors as homologous when Prum's character definitions matched my observations. Some complex behaviors that I observed showed obvious similarities to behaviors described by Prum (1990) but could not be directly scored as homologous characters. For example, one complex display (backward wing-flash) has similarities in body posture, wing movement, display location, and orientation to backward dance displays performed by members of the genus *Pipra*. In his analysis, Prum (1990) separates the backward dance displays of *Pipra* into several behavioral characters that define clades within *Pipra*. However, the display of the Club-winged Manakin, although similar, cannot be considered directly homologous with any of the backward dance characters because the details of the display are intermediate between discrete characters of Prum (1990). In such cases, I created new characters by breaking the composite behaviors of Prum (1990) into smaller, simpler characters that would more precisely capture behavioral homology. I created a separate data matrix for these recoded characters.

For phylogenetic analysis, I selected 11 species of manakins to represent each of the clades that might share the most recent common ancestor with the genus *Machaeropterus* and then reviewed the descriptions of display behaviors from the literature for each

of these species to assess homology with the newly created recoded characters. The 11 species were *Masius chrysopterus* (Prum and Johnson 1987), *Manacus manacus* (Snow 1962a), *Lepidothrix coronata* (Skutch 1969), *Dixiphia pipra* (Snow 1961), *Pipra fasciicauda* (Robbins 1983), *P. filicauda* (Schwartz and Snow 1978), *P. aureola* (Snow 1963a), *P. cornuta* (Snow 1977), *P. mentalis* (Skutch 1949, 1969), *P. rubrocapilla* (Sick 1967), and *P. erythrocephala* (Lill 1976, Snow 1962b).

I used the new behavioral data from Club-winged Manakins in three combinations to form three different data matrices for phylogenetic analysis: (1) the recoded behavioral data set, containing only the 15 atomized behavioral elements relating primarily to a backward wing-flash display (described below); (2) the combined behavioral data set containing all 42 behavioral characters resulting from the combination of the recoded characters with Prum's (1990) behavioral data set less the characters that were recoded (characters 4 and 9 to 15 from Prum [1990]); and (3) the total-evidence data set, containing 84 characters resulting from the combined behavioral data set and Prum's (1992) syringeal data set for the species of interest.

I determined the most-parsimonious phylogenetic arrangements of the three data sets using a branch-and-bound search in PAUP 3.1.1 (Swofford 1993). Because neither tyrannids nor cotingids, the nearest relatives of piprids, share the behavioral elements of piprids in any detail, I created a hypothetical outgroup that did not share any of the derived behavioral character states defined in the recoded behavioral data matrix. Otherwise, I retained the outgroup states coded by Prum (1990, 1992). The most-parsimonious trees were collapsed into strict-consensus trees for each data set. To indicate the amount of branch support, I computed Bremer values (Bremer 1994) with TreeRot (Sorenson 1996) for one of the two most-parsimonious trees resulting from analysis of the total-evidence data set.

RESULTS

GENERAL OBSERVATIONS AT THE LEK

Male Club-winged Manakins began displaying around 0600, although timing varied as much as 30 min among days. The single all-day watch showed that activity was highest after dawn and declined sharply by mid-morning, with occasional bouts of activity occurring throughout the rest of the day (Fig. 2). The relative frequency of individual display types is described below after the display descriptions.

Lek-breeding birds often defend individual courts or territories within the lek aggregation. Prum (1994) characterized the spatial organi-

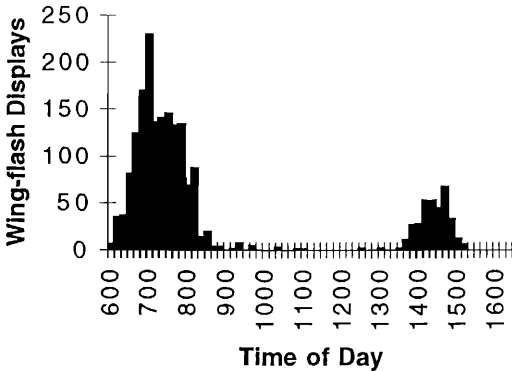


FIG. 2. Frequency of wing-flash displays heard at a lek of Club-winged Manakins every 10-min period between 0600 and 1630 EST on 30 October 1996.

zation of displaying male Club-winged Manakins as a dispersed lek ("male territories of 10 to 40 m in diameter with 2 to 7 adjacent male territories in a lek"), which is corroborated by my observations. Individual males moved and displayed within territories approximately 25 m in diameter. These territories were defended through displays from intrusions by other males. Territories were more or less linearly arranged along the length of the ravine. I heard up to six individuals advertising at one time, indicating that this lek had at least six males associated with it.

Displays were performed 1 to 20 m above the ground, most frequently just below the canopy (15 to 20 m), and often were easily visible from below. Most of the perches were exposed horizontal stems or branches about 1 cm in diameter. Each male used numerous perches for display and moved among perches frequently. In the course of one 60-min observation period, one male switched perches at least 56 times; this frequency seemed typical of most of the males that I observed for shorter periods. Perch use was not random within territories in that certain regions of the territory, and certain sets of perches, were used with greater frequency than others.

I observed nine male-male encounters in which territory borders were crossed. The wing-flash display was the principal display in these encounters, augmented by exaggerated lateral springs and numerous jump-turns (see below). I observed up to three males perching on the same branch, jump-turning and wing-flashing alternately in front of one another. The

effect of the aggregated and stereotyped displaying was to make the displays *appear* to be coordinated. However, the intensified aggression exhibited during these encounters makes coordination seem unlikely.

I observed no females during these encounters, nor did I observe females visiting other displaying males. Consequently, displays specific to courtship may exist that were not observed. However, several periods of heightened display activity suggested the presence of females. Efforts to capture male displays on video tape may have compromised my ability to detect females at the lek.

I observed foraging birds on four occasions, all involving consumption of melastome fruits. The birds fluttered next to berry clusters while plucking fruits, sometimes landing on boughs to eat directly. On two occasions, I observed a bird that had been preening while perched opportunistically snap at and catch insects that had flown within its reach.

MALE DISPLAY BEHAVIORS

I recognize six distinct display behaviors of male Club-winged Manakins: the wing-flash, the backward wing-flash, the crouch-call, the wing-presentation display, the jump-turn, and the lateral spring. These behaviors are described in detail below.

Wing-flash.—The wing-flash display is a combined visual and acoustic display and is the most frequently used display on the lek, functionally replacing vocal advertisement. The display involves a series of motions in which the wings are flicked (producing a brief mechanical *tick*) and then flipped (producing a sustained mechanical *ting*) above the back to produce a striking visual display (Figs. 3A and 3B).

The male usually begins by producing one or two *ticks* by a very rapid and subtle series of movements. First, he extends his legs and raises his rump in a rocking motion. Then, he flicks his wings up and outward in an extremely rapid motion that produces the sharp *tick*. The flicks are so rapid that one usually can only see a slight opening of the wings about 15° above the plane of the male's back in frame-by-frame analysis of high-speed (at least 1/250 s) videotaped displays. After the *ticks*, the male lowers his rump and returns his wings to a normal

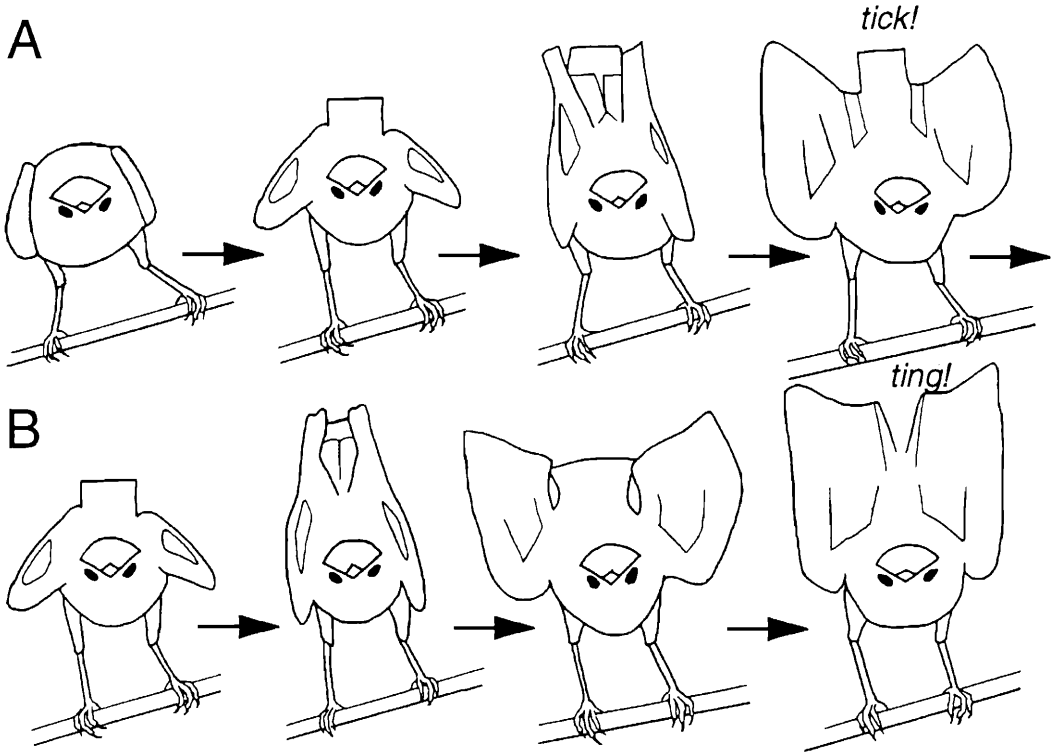


FIG. 3. Temporal sequence of body and wing postures assumed for the production of (A) a mechanical *tick* and (B) a mechanical *ting* in a wing-flash display. Sequence (A) may be repeated two or three times before entering into sequence (B). Sketches taken from video recordings.

resting posture, but his body remains horizontal.

Following the *ticks*, the male produces a longer-duration *ting*, or wing flip. The male initiates the *tings* in a manner similar to the *ticks*. He extends his legs, rocking his rump up, and then opens his wings slightly, drooping them down to his sides as the legs are extended. Then, in a movement lasting less than 0.017 s (the interval between video frames), he pronates his forearm, so that the secondaries are flung dorso-cranially above the plane of the back, and the *ting* commences. For the duration of the *ting*, the wings are positioned such that the secondaries are spread open, the primaries are closed, the wing surface is rotated 90° from that of a soaring position so that the leading edge is depressed, and the distal tips of the secondaries are elevated (Fig. 4). The wings do not contact each other. This open-winged posture is held for the duration of the *ting* while the bill is closed, the tail fanned, the plumage is sleeked, and the body is motionless. The wings,

however, vibrate slightly, and the secondaries move back and forth, parallel to the plane of the wing. The wing-shivering and feather oscillations are only perceptible on video with frame speeds of 1/250 s or less; to the unaided eye, the opened wings look slightly blurry during the *ting*. The display ends when the wings are rotated back down, swung low and out to the sides, and then closed to a resting position. The mechanical sound ceases as the bird resumes a normal perching posture.

The two mechanical sounds produced during the display are distinctive: one a *tick* produced by wing flicks, the other a *ting* produced when the wing is flipped over the back. Although these sounds are quite different to the human ear (*ticks* sound like two wooden chopsticks being hit together, and *tings* sound more like a toy horn), acoustically they differ only in duration (Fig. 5).

The two mechanical sounds in this display are always ordered such that zero to three brief introductory *ticks* are followed by one longer

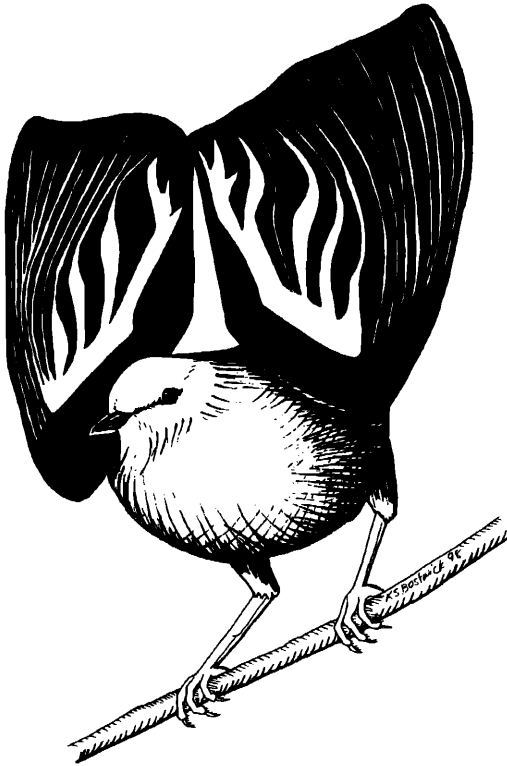


FIG. 4. Position of the wing during the production of the mechanical *ting* of the wing-flash display. The curved white markings on the wings are the barbs of the secondary feathers.

ting (Fig. 5A). In 200 video-recorded wing-flash displays, 6 had zero, 98 had one, 94 had two, and 2 had three introductory *ticks*. Displays with one *tick* are used most frequently during periods of reduced wing-flash frequency, whereas two *ticks* are used more often during periods of increased frequencies of displays. During periods of increased activity, a lateral jump often is inserted between the first and second *ticks* (see below).

Differences within and between individuals in the timing and duration of the *tick* and *ting* elements are undetectable to the human ear. In displays with two *ticks*, the average time between the onsets of the first and second *ticks* was $593.0 \pm \text{SD of } 49.9$ ms for one male and 622.1 ± 49.2 ms for the other; the time between the second *tick* and the *ting* was 316.3 ± 8.0 ms and 324.5 ± 8.7 ms in the two males, and the *ting* lasted 333.1 ± 26.8 ms and 364.4 ± 13.8 ms, respectively ($n = 20$ for each male).

The acoustic structure of the mechanical sounds produced by Club-winged Manakins is unique (Prum 1998). Each sound is composed of a series of harmonically related pure tones. That is, the lowest (fundamental) frequency tone is accompanied by tones of higher frequency (harmonics) that are related as integer multiples. The average frequencies of the fundamental tone and first three harmonics were 1.48 ± 0.04 , 2.93 ± 0.04 , 4.41 ± 0.05 , and 5.89 ± 0.06 kHz, respectively, for one male and 1.44 ± 0.08 , 2.92 ± 0.06 , 4.37 ± 0.08 , and 5.88 ± 0.08 , respectively, for the other ($n = 20$ for each male). This acoustic structure is represented graphically by the successive horizontal bars in the spectrograms in Figure 5.

Backward wing-flash.—The backward wing-flash is the most behaviorally complex display that I observed, being relatively long in duration and composed of numerous distinct elements, including mechanical sounds. Males assume a stereotypic posture and perform backward hitching (leg-direction-exchange hops) and/or jump-turns (see below), all of which culminate in a pair of mechanically produced *tings* (Fig. 6A).

The display is performed on horizontal or inclined branches. The male orients at an angle oblique to the perch (head down the incline if perch is angled) and bows forward with his legs extended so that his breast nearly touches the perch. The head is lowered and the neck extended so that the bill is parallel to body's main axis, and the feathers are sleeked against the body.

In this posture, the bird hops backward on the perch, moving upward if the perch is inclined. The hops are short (<3 cm), rapid, and low (with almost no vertical displacement). The feet alternate left-foot-front, right-foot-front with each hop. During the backward hops, the wings are held slightly out from the body and shivered. After two to six backward hops ($n = 8$), the bird freezes momentarily, still in the bowed posture, and then produces two mechanical *tings* in close succession by throwing the secondaries into the same position described in the wing-flash display. With the wings then closed back into the shivering position, the display may continue with additional backward hops, and additional double *tings*. In 20 audio- and video-recorded bouts of the backward wing-flash, 12 had one set of double

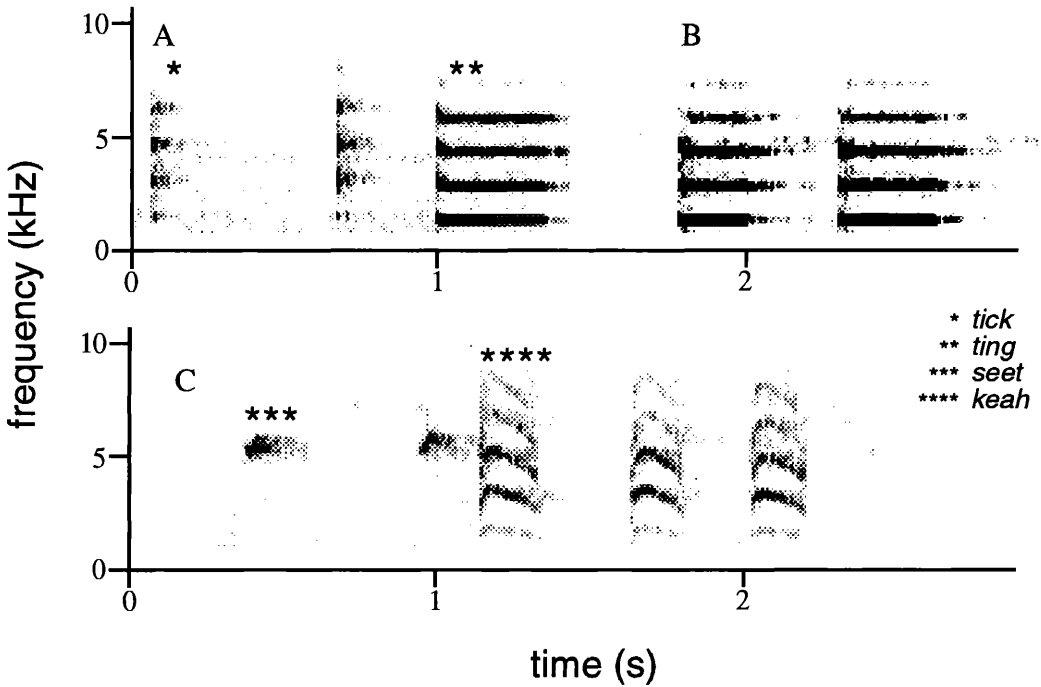


FIG. 5. Spectrograms of mechanical and vocal sounds of male Club-winged Manakins: (A) *tick*, *tick-ting* of the wing-flash display; (B) double *ting* of the backward wing-flash display; (C) two *seets* and three *keahs* of the crouch-call display.

tings, 2 had two, 3 had three, 1 had four, and 1 had six. After the last set of *tings*, the leaning posture and shivering wings are resumed for a moment more. The display ends as the bird straightens up and relaxes its plumage.

Twice I recorded a variation of this backward wing-flash on video. A 180° jump-turn was inserted into the hopping phase of the dance, after which the bow and backward hopping were resumed. The effect of inserting a jump-turn

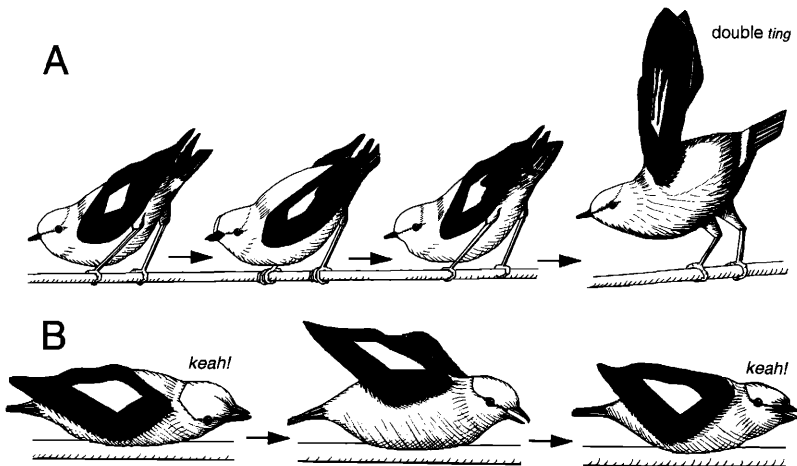


FIG. 6. Two display behaviors of Club-winged Manakins: (A) the backward wing-flash display, showing the production of a mechanical *ting*; (B) the crouch-call display, showing body posture and timing of calls.

was to change the direction in which the dance proceeded. In both cases, extended backward movement of the bird was prevented by perch obstacles (a fork in the perch, or a stem or branch of the tree) such that the jump-turns allowed the dance to be performed continually in the small amount of space available.

The mechanical *tings* in the backward wing-flash display are identical to those in the wing-flash display in the acoustic structure of frequencies and the wing posture assumed for production. However, they are (1) never preceded by *ticks*, (2) always doubled or rarely tripled, and (3) shorter in duration (first *ting* = 201 ± 25.2 ms; second *ting* = 234 ± 33.0 ms, $n = 4$; Fig. 5B). Also, the *tings* are initiated with the male in a breast-down, rump-up posture; thus, no rocking motion is associated with their production.

Crouch-call.—A series of stereotyped movements is associated with the production of loud vocalizations made by territorial males. Initially, while at rest the male is perched upright and oriented perpendicular to the perch. Usually (12 of 17), the display begins with a high-pitched *seet* or *seet-seet* call. The male then twists his body parallel to his perch, leans forward, lowers his head to one side or the other of the perch, and emits a loud *keah!* He proceeds to call while lowering his head alternately to the left and right sides of the perch with a single closed-wing wing-flap punctuating each call and to-and-fro movement of the head (Fig. 6B). After one to eight calls in a row ($\bar{x} = 4.25$, $n = 55$ audio or video recordings), the male resumes a normal posture and the display ends. I never witnessed the vocalization ($n > 20$ visual and video observations) without the accompanying display motions, nor did I hear *seet* calls outside of the context of this display.

The acoustic structure of these vocalizations is shown in Figure 5C. The *seet* calls are simple single notes with frequencies between 4.6 and 5.6 kHz and a duration of approximately 0.1 s. The *keah* calls are composed of 5 to 6 harmonic bands (the highest band is occasionally lost) that increase abruptly and then decrease more slowly in frequency. The fundamental frequency ranges from 1.4 to 1.8 kHz. Each *keah* note lasts around 0.2 s, and the pauses between *keah* notes are between 0.2 and 0.3 s in duration.

Wing-presentation.—This display contains no acoustic elements. While oriented perpendicu-

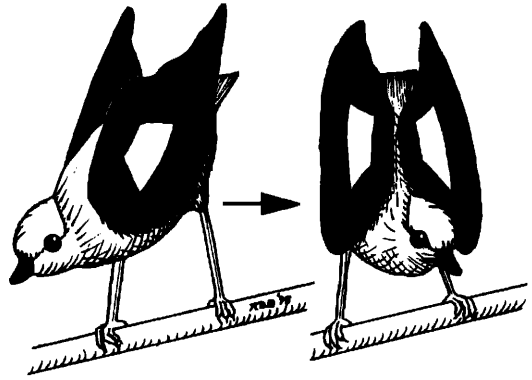


FIG. 7. The wing-presentation display of Club-winged Manakins.

lar to the perch, the male bows forward such that the strong black-and-white markings on the dorsal surface of his wings are visible when viewed head on. The legs are extended, and the head and breast are bowed down, or lowered, in a posture similar to that assumed in the backward wing-flash described above. With the bill pointed along the main axis of the body and the plumage sleeked, the male slowly, stiffly, and jerkily rotates his torso to one side and then the other, as if to display the black-and-white wing markings to his left and right sides (Fig. 7). He enacts this display for no more than 5 s, at which point he straightens up and relaxes his plumage, thus ending the display.

Jump-turn.—This is a simple display in which the bird jumps vertically into the air and rotates 180°, coming down facing in the opposite direction. The jumps are about 4 cm in height, and the bird lands 5 to 15 cm lateral to where he began the jump. A soft *tick*, acoustically structured like normal *ticks* but noticeably weaker, is often produced (10 of 20 displays recorded on video) by rapid wing flicks immediately preceding the jump and turn. Otherwise, the wings remain closed during the jump. These displays may occur between wing-flash displays or when the bird is otherwise perched.

Lateral spring.—In this relatively simple display, the bird springs nearly horizontally 20 to 30 cm down the length of his display perch. This element was observed most frequently inserted into the wing-flash displays, immediately following the first *tick* and just prior to the second *tick* element (20 of 21 lateral-springs sampled from video).

One male performed a jump with a 180° turn

TABLE 1. Potential homologous behavioral elements between Club-winged Manakins and other Pipridae.

No.	Character ^a
1	PC3, Chin-down posture. Similar to posture assumed during wing-presentation and backward wing-flash displays.
2	PC16, Wing-shiver log display. Similar to posture assumed during wing-presentation and backward wing-flash displays.
3	PC4, Horizontal posture. Similar to posture adopted during crouch-call display.
4	PC7, About face. Similar to jump-turn.
5	PC9, Backward-slide display. Many details similar to backward wing-flash display.
6	PC 10, Backward-slide display with forward rebound. Many details similar to backward wing-flash display.
7	PC11, Side-to-side slide. Similar to lateral springs.
8	PC12, Side-to-side jump display. Similar to lateral springs.
9	PC13, Stationary display. Similar to posture assumed during backward wing-flash display and wing-presentation display.
10	PC14, Wing-shiver display. Similar to posture assumed during backward wing-flash display and wing-presentation display.
11	PC15, Wing-shiver twist display. Similar to posture assumed during backward wing-flash display and wing-presentation display.
12	PC30, To-and-fro with mechanical wing noise. As described by Prum (1990).
13	PC44, Display arena of multiple horizontal twigs. As described by Prum (1990).

^a Character numbers (PC) and names from Prum (1990), followed by the potentially homologous behavior described herein.

(like a jump-turn) that was as long as that of a lateral spring in length and was inserted into the wing-flash display between the two *tings*. I observed this combined lateral spring/jump-turn twice during the same sample period as the 20 jump-turns and 21 lateral springs above.

DISPLAY FREQUENCIES

Of the acoustically detectable displays, I observed the crouch-call and the backward wing-flash much less frequently than the wing-flash. Among all of the members of the lek, the wing-flash display was performed an average of 64.5 times per 10-min sample period, compared with 1.2 for the crouch-call display and 1.0 for the backward wing-flash dance display ($n = 18$ 10-min periods between 0630 and 0930). In a 1-h sample between 0650 and 0750 (a period of high activity), one male performed the wing-flash 180 times, the crouch-call 10 times, and the backward wing-flash such that the double *ting* was heard 12 times.

I observed jump-turns and lateral springs with approximately equal frequency relative to each other: 20 jump-turns to 21 lateral springs in 1 h of display video. Lateral springs and jump-turns occurred most often during periods of increased activity when a male changed perches frequently and when frequent wing-flash displays were being performed by adjacent, presumably territorial, males. I witnessed

the wing-presentation display only four times during the entire study period. This infrequent observation perhaps was due in part to the display's brevity and its lack of an acoustic component.

PHYLOGENETIC ANALYSIS

I considered 13 of the behavioral characters delineated by Prum (1990) to be similar enough to those described herein for Club-winged Manakins to merit consideration of homology (Table 1). Three characters, about faces (character 4), to-and-fro with mechanical wing noise (character 12), and display arena of multiple horizontal twigs (character 13), were observed in the Club-winged Manakin and were already considered homologous in Prum's (1990) analysis (see Table 1). Therefore, coding for these characters was not changed in this analysis (they are accounted for in the combined behavioral data set). Two characters, the chin-down posture (character 1) and the wing-shiver log display (character 2), were not considered homologous to Club-winged Manakin behaviors owing to lack of detailed similarity. These behaviors, found variously in members of the *Ilicurini* (*Masius*, *Ilicura*, and *Corapipo*; Prum 1990, Théry 1990), have been described as "crouches" where the belly is lowered and the wrists are raised. They are performed on fallen logs often after very stereotypic flight displays.

TABLE 2. Recoded character name and states used in parsimony analysis. Characters are unordered and refer to behaviors used by adult male manakins in displays.

No.	Character
1	Backward posture: 0, absent; 1, body oriented oblique or parallel to display perch, inclined forward (head low, legs stretched), and oriented with the rump or cloacal region toward a proximal male or a female (distinguished from PC 16, wing-shiver log display).
2	Tail position associated with backward posture (character 1, state 1): 0, not applicable; 1, elevated; 2, depressed.
3	Backward motion: 0, absent; 1, present in repertoire; 2, present with backward posture (character 1, state 1) creating a "backward dance."
4	Wing activity associated with backward dance (character 3, state 2): 0, not vibrated; 1, vibrated.
5	Pivot around planted foot: 0, absent; 1, present in repertoire.
6	Hitching (leg-direction-exchange hops) backward down perch: 0, absent; 1, present with backward dance (character 3, state 2).
7	Sliding (small rapid steps that give the appearance of a sliding or gliding motion): 0, absent; 1, present in repertoire; 2, present with backward dance (character 3, state 2).
8	Wing posture associated with backward dance (character 3, state 2): 0, not applicable; 1, low / drooped; 2, raised slightly.
9	Wing spread during backward dance (character 3, state 2): 0, absent; 1, wings spread horizontally at intervals.
10	Wing elevation associated with backward dance (character 3, state 2): 0, absent; 1, wings raised above back; 2, wings raised above back with a mechanical sound.
11	Tail posture associated with backward dance (character 3, state 2): 0, closed; 1, fanned.
12	Tail activity associated with backward dance (character 3, state 2): 0, none; 1, vibrated; 2, switched across the face of a visitor.
13	Tail punctuation associated with backward dance (character 3, state 2): 0, absent; 1, depressed and fanned at end of backward motion.
14	Side-to-side motion or display: 0, absent; 1, lateral motion perpendicular to the perch.
15	Gait or means of side-to-side motion (character 14, state 1): 0, not applicable; 1, hops; 2, leaps; 3, slides.

The wing-shiver log display involves a backward walk, rather than hop or slide, with alternating motions of the wings (Prum 1990, Théry 1990). In contrast, Club-winged Manakins do not display on fallen logs or immediately following flight displays, and they do not raise their wrists nor move their wings alternately in any of their displays. In displays with bowed posture and backward movement, Club-winged Manakins hop backward rather than walk. For this reason, these two characters were left as coded in Prum's (1990) original analysis as not homologous, and were considered no further. The remaining eight characters from Table 1 (representing characters 4 and 9 to 15 in Prum [1990]) were recoded into 15 characters (Table 2) and analyzed as the recoded behavioral data set (Appendix).

The recoded behavioral data set produced two most-parsimonious trees with tree length (TL) = 28, consistency index (CI) = 0.857, and homology index (HI) = 0.143. Both trees placed the Club-winged Manakin as the sister to a clade composed of (*Pipra cornuta*, (*P. mentalis*, *P. erythrocephala*, and *P. rubrocapilla*)) (Fig. 8A).

The combined behavioral data set resulted in 12 most-parsimonious trees with TL = 62, CI = 0.871, and HI = 0.129. Finally, the total-evidence data set resulted in two most-parsimonious trees with TL = 116, CI = 0.784, and HI = 0.216. In the combined behavioral and the total-evidence data sets, all most-parsimonious trees placed the Club-winged Manakin as the sister to *Pipra* (Figs. 8B and 8C) and yielded relationships among members of *Pipra* consistent with those reported by Prum (1992). Bremer branch-support values for one of two most-parsimonious total-evidence trees are shown on Figure 8C.

DISCUSSION

Display repertoire.—The display repertoire of Club-winged Manakins is more diverse than previously recognized. This species has a repertoire of at least four mechanical phrases (soft ticks, ticks, tings, and double tings), two vocal sounds (*seets*, *keahs*), and seven display behaviors (wing-flash, crouch-call, backward wing-flash, wing-presentation, jump-turn, and lat-

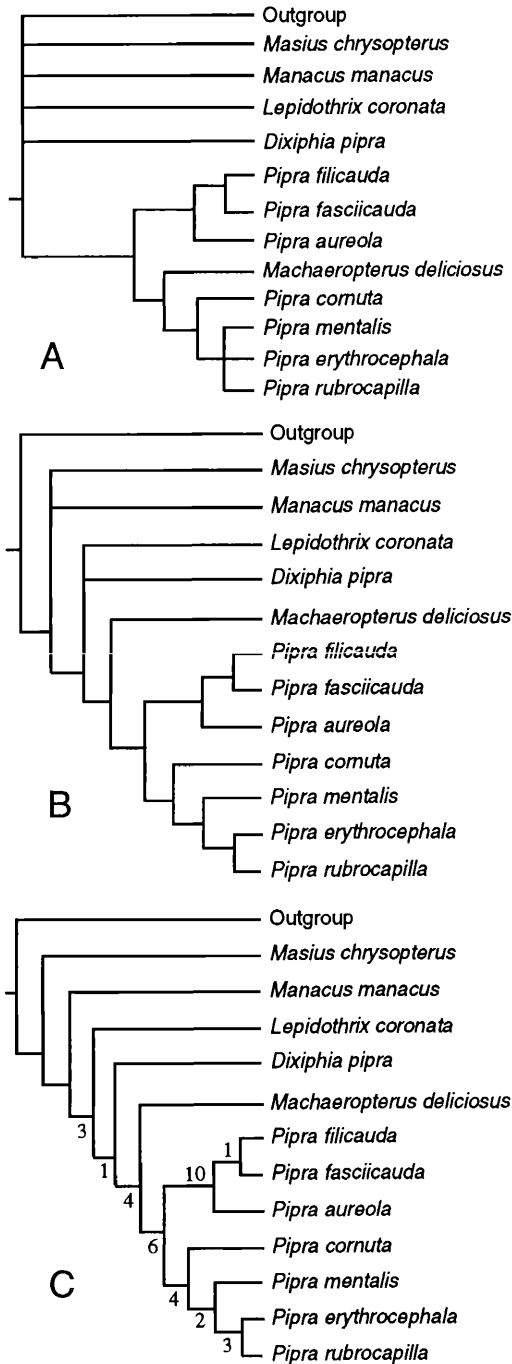


FIG. 8. Cladograms representing relationships between representative members of Pipridae generated using increasingly inclusive data sets. (A) The recorded behavioral data set (consensus of two most-parsimonious trees). (B) The combined behavioral data set (strict consensus of 18 most-parsimonious trees). (C) the total-evidence data set (one of two

eral spring, and the pseudo-copulations described by Orejuela et al. [1982]).

Orejuela et al. (1982) mentioned a vocalization that was associated with copulations and pseudo-copulations. I observed neither copulations nor pseudo-copulations. The vocalization observed in association with the crouch-call display matches the description of the vocalization described by Orejuela et al. (1982), but the display motions I witnessed in association with the vocalization were not noted.

Mechanical sounds.—Although the production of intentionally modulated mechanical sounds is a relatively rare trait among passerines, its evolution has been dynamic in piprids (Prum 1998). According to Prum's phylogenetic hypotheses, mechanical sounds in displays have been derived independently four to six times, with subsequent diversification of mechanical sound repertoires in several clades of the Pipridae (Prum 1998).

The mechanical sound production of Club-winged Manakins is exceptional even among manakins. The species' mechanical sound repertoire includes four distinct phrases that differ in duration, timing, and the contexts in which they are used. Only the genus *Manacus* has a comparable repertoire. The large repertoire of Club-winged Manakins emphasizes the dynamic nature of sexual selection on mechanical sounds as an alternative mechanism of communication.

Functionally, mechanical sounds of Club-winged Manakins have replaced vocal advertisement on the lek. In most manakins, the male announces his presence on his territory by frequent production of a simple vocalization termed an "advertisement" call (Sick 1967). Club-winged Manakins are unique in that the mechanical sound produced by the wing-flash display has replaced vocalizations as the primary means of territorial advertisement. This is evident from observations that the wing-flash is the most frequently used display and is the *only* display or sound used during periods of intermittent activity. The mechanical sounds from this display are audible for dozens of me-

←
most-parsimonious trees). Bremer values indicate amount of branch support on total-evidence tree (C).

ters, allowing even noncontiguous territories to be in acoustic contact.

The mechanical sounds of Club-winged Manakins are acoustically unique. Although at least 18 of the more than 40 species of manakins produce mechanical sounds, nearly all of them are either snaps (extremely brief, broad-frequency sounds) or a series of snaps (Prum 1998). The acoustic structure of the mechanical sounds of Club-winged Manakins is long in duration and has harmonically related pure tones, which implies a unique mechanism of production. The physical mechanism(s) by which the mechanical sounds are produced is the subject of current research.

Phylogenetic analysis.—The new behavioral information yields two alternative and previously unproposed hypotheses of relationships. The recoded data set, which primarily codes behaviors relating to the backward wing-flash dance, places Club-winged Manakins sister to a clade composed of *Pipra cornuta*, *P. mentalis*, *P. rubrocapilla*, and *P. erythrocephala* (and probably *P. chloromeros*, not included in this study), which is also known as the *Pipra erythrocephala* superspecies group (Haffer 1970), or the *Ceratopipra* subgenus (sensu Prum 1992). This result is supported by an extensive mitochondrial DNA phylogeny of the family (S. Hackett pers. comm.). If *Pipra* (sensu Prum 1992) is paraphyletic, as these results suggest, a revision of the classification of this group is necessary. The alternative hypothesis, based on the results of the total-evidence data, places Club-winged Manakins sister to a monophyletic *Pipra*. In either case, my results suggest that *Machaeropterus* is more closely related to *Pipra* than previously thought.

These two new hypotheses of relationships between *Machaeropterus* and *Pipra* have several implications. Morphologically, in Prum's syringeal analysis (1992), five characters are derived between a basal polytomy in which the genus *Machaeropterus* was placed and a position basal to a monophyletic *Pipra* (Fig. 1). One of these five syringeal characters (character 7; Prum 1992) is shared between Club-winged Manakins and *Pipra* and would now be reinterpreted as a synapomorphy of the *Machaeropterus* + *Pipra* clade. Another (character 15; Prum 1992) is polymorphic in Club-winged Manakins, with some individuals expressing an intermediate state in a character-transition series that with

equal parsimony would place Club-winged Manakins as the sister of *Pipra*. The other three characters (2, 3, 54.1; Prum 1992) conflict with this new hypothesis and would have to be considered reversals in *Machaeropterus*. The alternative placement of *Machaeropterus* as sister to the *Pipra erythrocephala* superspecies group would imply further syringeal character reversal. Such hypotheses of character reversals may be explained by the extreme reduction in the syringes of species of *Machaeropterus* (Prum 1992).

Behaviorally, this hypothesis implies the backward dances of *Pipra* are homologous with the backward wing-flash dance of Club-winged Manakins and that these displays originated before *Machaeropterus* diverged from members of *Pipra*. If *Machaeropterus* is monophyletic, as strongly suggested by plumage, syringeal (Prum 1992), and morphological data (K. Bostwick unpubl. data), we would expect to find a backward dance in both congeners, the Striped Manakin (*M. regulus*) and the Fiery-capped Manakin (*M. pyrocephalus*). No backward dance has been observed in either of these species during recent field research. However, few behavioral similarities exist between Club-winged Manakins and the other two members of *Machaeropterus* (pers. obs., R. O. Prum pers. comm.). Therefore, if the genus *Machaeropterus* is monophyletic, either extensive behavioral convergence of Club-winged Manakin displays with those of *Pipra* has occurred, and the relationship proposed here is spurious, or behavioral reversal and/or modification has been so extensive within *Machaeropterus* that the backward dance is either unrecognizable or absent in the Striped and Fiery-capped manakins.

A monophyletic *Machaeropterus* + *Pipra* clade has implications for understanding the evolution of mechanical sounds. First, members of the genus *Pipra* create simple snaps with their secondaries, and the Striped and Fiery-capped manakins produce wing sounds with modified secondaries (K. Bostwick unpubl. data, Sick 1967). Thus, the production of mechanical sounds by modified secondaries probably evolved before the split between *Machaeropterus* and *Pipra* and therefore is likely to be homologous between members of these genera.

Second, the behavioral origins of the mechanical sounds produced by Club-winged Manakins can now be explored. For instance,

the mechanical sounds originally may have evolved as an elaboration of the backward dance. Several members of *Pipra* embellish their backward dances with wing movements that include wing flicks and flips into horizontal and vertical positions. One species, the Scarlet-horned Manakin (*P. cornuta*), produces a mechanical *whirr* with its secondaries at the end of its backward dance (Snow 1977). After incorporation into the backward dance, the mechanical sound subsequently may have been co-opted for use as an advertisement, resulting in the prominent wing-flash display that functionally replaced the vocal advertisement call. Alternatively, the complex mechanical sounds of the Club-winged Manakin may have evolved in the context of an advertisement and subsequently been inserted into the already existing backward dance after *Machaeropterus* and *Pipra* diverged. These alternative hypotheses of evolution of the unusual mechanical sounds found in Club-winged Manakins can now be proposed more explicitly and explored more thoroughly as more detailed behavioral data are gathered and the group's phylogeny is further resolved.

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