

LEK STRUCTURE AND MALE DISPLAY REPERTOIRE OF BLUE-CROWNED MANAKINS IN EASTERN ECUADOR

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Abstract. Among lek-breeding manakins (Pipridae), courtship repertoires are extremely diverse and have played a central role in establishing phylogenetic relationships within the family. Behaviorally, *Lepidothrix* is among the least known genera in the family, with brief accounts published for only two of the eight species. Here, I describe the lek structure, territory characteristics, vocalizations and behavioral display elements of the Blue-crowned Manakin (*Lepidothrix coronata coronata*) in eastern Ecuador. From 2003 to 2006, I located all leks in two 100-ha study plots (average of 13.5 leks 100 ha⁻¹) and recorded behavior at individual territories in ten leks. Males displayed solitarily or at exploded leks with up to seven individual territories of ~0.1 ha; within a lek, territory centers were separated by about 90 m. Males in definitive and predefinitive plumage (2 years and older) held stable territories, whereas first-year, female-plumaged males did not hold stable territories but sometimes associated loosely with territorial males. I noted 4 vocalizations and 11 male display behaviors during solitary and group displays involving other males and females, revealing a repertoire considerably more diverse than previously documented.

Key words: Blue-crowned Manakin, courtship, display behavior, Ecuador, lek, *Lepidothrix coronata*, Pipridae.

Estructura de las Asambleas de Cortejo y Repertorio de Despliegue de los Machos de *Lepidothrix coronata* en el Oriente de Ecuador

Resumen. Los repertorios de cortejo son extremadamente diversos entre los saltarines (Pipridae) que se reproducen en asambleas y han desempeñado un papel central en el establecimiento de las relaciones filogenéticas entre miembros de la familia. *Lepidothrix* es uno de los géneros peor conocidos de la familia en términos de su comportamiento, pues se han publicado recuentos breves sólo para dos de las ocho especies. En este estudio, describo la estructura de las asambleas de cortejo, las características de los territorios, las vocalizaciones y los elementos de comportamiento de los despliegues de *Lepidothrix coronata coronata* en el oriente de Ecuador. Entre 2003 y 2006, ubiqué todas las asambleas de cortejo en dos parcelas de estudio de 100 ha (promedio de 13.5 asambleas 100 ha⁻¹) y registré el comportamiento de los individuos en sus territorios en diez asambleas. Los machos hicieron despliegues solitarios o en asambleas dispersas que comprendían hasta siete territorios individuales de ~0.1 ha; dentro de cada asamblea, los centros de los territorios estuvieron separados por unos 90 m. Los machos con plumaje definitivo o predefinitivo (de 2 años de edad o mayores) mantuvieron territorios estables, mientras que los machos del primer año con plumaje de hembra no tuvieron territorios estables, aunque ocasionalmente se asociaron débilmente con machos territoriales. Registré 4 vocalizaciones y 11 comportamientos de despliegue en los machos durante despliegues solitarios y en grupos que incluían otros machos y hembras. Este repertorio es considerablemente más diverso que el documentado anteriormente.

INTRODUCTION

Manakins (Pipridae) are small-bodied, neotropical frugivores characterized generally by marked sexual dimorphism and a lek-based breeding system with complex male courtship displays (Sick 1967, Lill 1976, Prum 1990, Snow 2004). Their extremely diverse courtship repertoires are believed to have evolved largely under intersexual selection (Prum 1997) and hold phylogenetic information that has been instrumental

in reconstructing historical relationships within the family (Prum 1990, 1994, Prum and Johnson 1987, Bostwick 2000). The genus *Lepidothrix* (formerly included within *Pipra*) comprises some of the manakins least known behaviorally. Among the eight recognized species—*serena*, *coronata*, *isidorei*, *sua-vissima*, *caeruleocapilla*, *natterei*, *vilasboasi*, and *iris*—the display behavior of only the first two has been described in any detail (Skutch 1969, Prum 1985, 1994, Théry 1990). In addition, the taxonomy of the genus is not completely resolved.

Manuscript received 3 December 2008; accepted 17 June 2009.

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Although phylogenetic analyses of behavioral and morphological traits revealed the paraphyly of *Lepidothrix* in relation to *Pipra* (Prum 1992), later confirmed with molecular data (Rêgo et al. 2007), the relationship between *Lepidothrix* and other manakin genera is still debated (Prum 1990, 1992, Rêgo et al. 2007).

The Blue-crowned Manakin (*L. coronata*) is widespread in humid mature unflooded forests at elevations <1000 m in northwestern Amazonia, the Chocó region west of the Andes, and southern Central America (Ridgely and Tudor 1994, Snow 2004). The eight recognized subspecies vary largely in male plumage and somewhat in vocalization (Snow 2004), but large incongruences between genetic and phenotypic variation complicate resolution of the species' taxonomy (Chevion et al. 2005). In eastern Ecuador, *L. coronata coronata* is often ranked among the ten avian species captured most frequently in mist nets (Blake 2007). Leks are "dispersed" (sensu Prum 1994) and typically located along intermediate elevations and moderate slopes of upland forest (Loiselle et al. 2007, Durães et al. 2007). As in most manakins, in this species sexual dimorphism is marked and plumage maturation in males is delayed: females and first-year (juvenile) males are bright green; subadults (2 years old) have a predefinitive plumage that retains variable amounts of green, and only in their third year do males fully acquire the definitive plumage characterized by a sooty black body and bright blue crown (Ryder and Durães 2005).

The display repertoire of *L. coronata* seems to be limited in comparison to that of other manakins (Prum 1990). But our knowledge is restricted to few observations from populations mostly from Central America (Skutch 1969, Prum 1990). Furthermore, the diversity in plumage and songs observed across the species' range (Snow 2004, Chevion et al. 2005) suggests that display behavior may also vary geographically, as has been observed for *L. serena* (Prum 1985, Théry 1990). Thus a full account of the species' behavioral repertoire is currently lacking. Here I provide the first detailed account of the vocalizations and display behaviors of *L. coronata* as well as details on lek structure and spatial organization, based on a population in eastern Ecuador.

STUDY AREA AND METHODS

This study took place at Tiputini Biodiversity Station (0° 38' S, 76° 08' W, 190–270 m above sea level), Orellana Province, eastern Ecuador. The station covers 650 ha of virtually undisturbed habitat and is located within the 1.2 million-ha Yasuní Biosphere Reserve. The vegetation is lowland wet evergreen forest, both *terra firme* and *várzea*. I recorded data during the manakins' main breeding season in the region, from October or November of 2003, 2004, and 2005 to April of the following year (hereafter, 2004, 2005, and 2006 field seasons) at two 100-ha permanent study plots separated by ~1.5 km at their

nearest edges. For a more detailed description of the study area see Loiselle et al. (2007).

Each year, I located leks by systematically searching for vocalizing males throughout the plots. Once I located a vocalizing male, I made repeated visits to the site in order to (1) establish whether the male held a stable territory at the site, (2) search for other neighboring territorial males, (3) delimit boundaries of individuals' territories and leks, (4) capture and mark territorial males, and (5) conduct behavioral observations at focal territories. Territorial males were captured with mist nets, with or without the use of song playbacks, and tagged with uniquely numbered aluminum bands and plastic color bands. I mapped song perches and recorded their type (tree branch, liana, epiphyte, etc.), approximate height and diameter, and approximate diameter at breast height (DBH) of the tree. I plotted song perches in ArcGIS 9.1 (ESRI, Redlands, CA) and drew minimum convex polygons to define territory and lek boundaries. I considered territories to belong to the same lek when males were within auditory contact or when I observed occasional interactions among neighboring males. Despite relatively high turnover of males, locations of most leks were constant over the years (Durães et al. 2008). Intensive search for leks continued until no new displaying males could be detected and all leks and most territories in both study plots were mapped.

The manakins' behavior was observed at a subset of territories in one of the study plots in 2005 and 2006. In 2005, behavior was observed in 32 territories at 11 leks in 30-min sessions at early morning (0630–0900), mid-day (1000–1300), or mid-afternoon (1400–1600). In 2006, observations were conducted in 25 territories at 10 leks during 120-min sessions at early morning or mid-afternoon, the periods of highest display activity (Fig. 1). The two years combined, 38 individual males were observed (i.e., 19 individuals were observed in both years), each for an average of 132 ± 39 min in 2005 (total: 110 hr) and 713 ± 271 min in 2006 (total: 297 hr). Birds were observed with 10×42 binoculars and without the use of a blind. An observer sat at a position from which the display court of the focal male (see below) was visible but ≥ 5 m away and allowed 5 min to elapse before starting to manually record behaviors such as type of activity (e.g., calling, preening, foraging, etc.), type of display maneuvers and vocalizations, intraspecific interactions, etc. Green-plumaged birds interacting with the territory holder could be in most cases identified as juvenile males or females by their behavior (see Male–Female Interactions); in several cases the identification was later confirmed by molecular sex determination in the laboratory (Ryder and Durães 2005). Data on vocalization and movement rates presented here were taken in 2006, when I recorded the number of different types of vocalizations given and the number of times the bird changed song perches during continuous focal observations for 10-min intervals. During additional visits to leks, I recorded vocalizations in uncompressed

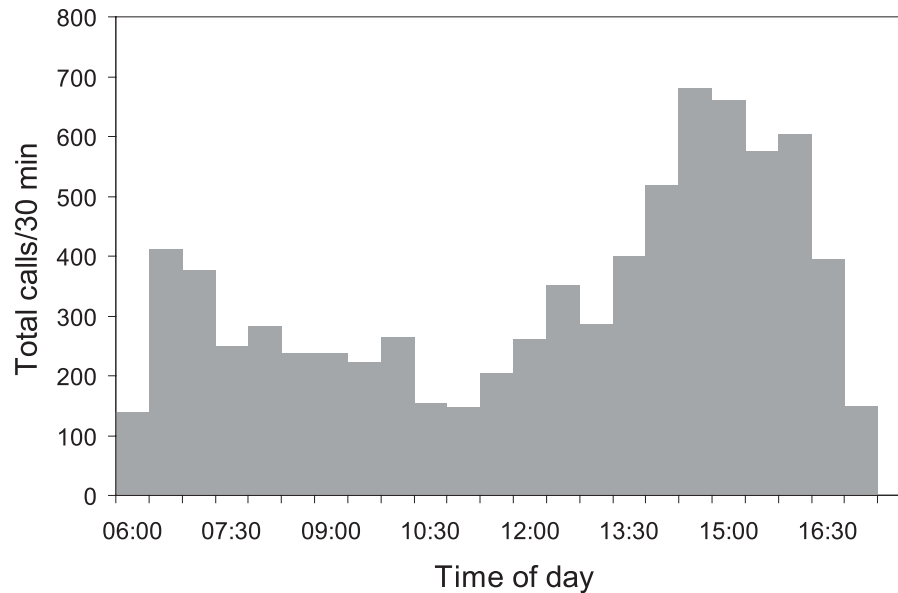


FIGURE 1. Temporal distribution of vocalization during daylight at leks of the Blue-crowned Manakin (*Lepidothrix coronata*) in eastern Ecuador. Values represent total number of calls emitted at the lek every 30 min, averaged for two leks composed of three and four males, each observed for 12 consecutive hours in December 2003 and another 12 hours in February 2004.

pcm format with a Sony MZ-RH910 minidisk recorder and a Sunheiser ME-66 short-shotgun microphone, then prepared sound spectrograms in Raven Lite 1.0 for Windows (Charif et al. 2006). I measured characteristics (frequency, duration, etc.) of the first clear note of each type of song recorded from ten territorial males and describe display behaviors with the terminology adopted by Prum (1990). Throughout the paper unless otherwise stated, data are means \pm SD.

RESULTS

LEKS, TERRITORIES, AND DISPLAY PERCHES

I located 13 or 14 leks each year in each 100-ha study plot. The average nearest-neighbor distance between the leks' centroids was 200 ± 70 m. Males displayed solitarily or at leks of up to seven males' territories, with an average of 3.0 ± 1.6 territories per lek. Individual territories ranged in area from 200 to 5000 m², averaged 1000 m² (0.1 ha) and, within a lek, were separated by 91 ± 47 m between centroids. Most territories were contiguous, although in some cases they were separated by unoccupied intervening space.

Males in both definitive and predefinitive plumage held stable territories at leks (i.e., territories that were used and actively defended by individual males throughout at least one breeding season). Juvenile males did not hold stable territories but often established loose associations with territorial males (see below). Males defended territories against intruding males and attracted females by vocalizing from song perches. Song perches were horizontal or slightly angled thin branches of trees (62%, $n = 229$), horizontal portions of lianas (36%,

$n = 133$), epiphytes on trees (1%, $n = 3$), and others (vine tangles, fallen tree branches, vertical stems, 1%, $n = 3$). These perches were on average 4.4 ± 1.8 m above the ground (range 0.5–12 m, $n = 492$), 1.4 ± 0.9 cm in diameter (0.5–5 cm, $n = 312$), and were located in trees with DBH 5.3 ± 2.3 cm (1.5–10 cm, $n = 43$).

Within the territory, each male held at least one display court, a small area (~3–5 m diameter) in which it performed ritualized courtship displays and copulated close to ground level. Most males were observed using a single display court, although two of the 38 focal males occasionally used a second court within their territories. The location of the court within the territory was either maintained or changed the following year, probably according to microhabitat changes within the territory. Courts were in areas of relatively open understory dominated by thin twigs that were used as vertical perches during displays. In some cases, the court was an open area underneath a dense vine tangle. Males did not clear the ground below their display perches.

VOCALIZATIONS

During the breeding season, males vocalize actively from 06:00 to 17:30 (Fig. 1). Focal males vocalized in 95% of the 10-min observation blocks ($n = 1587$ blocks), responded aggressively to playback of conspecific songs, and moved among song perches at a rate of 0.25 ± 0.12 changes min⁻¹. The vocal repertoire included four distinct vocalizations, described below; call rates are given only in the context of observation blocks in which a particular call was recorded:

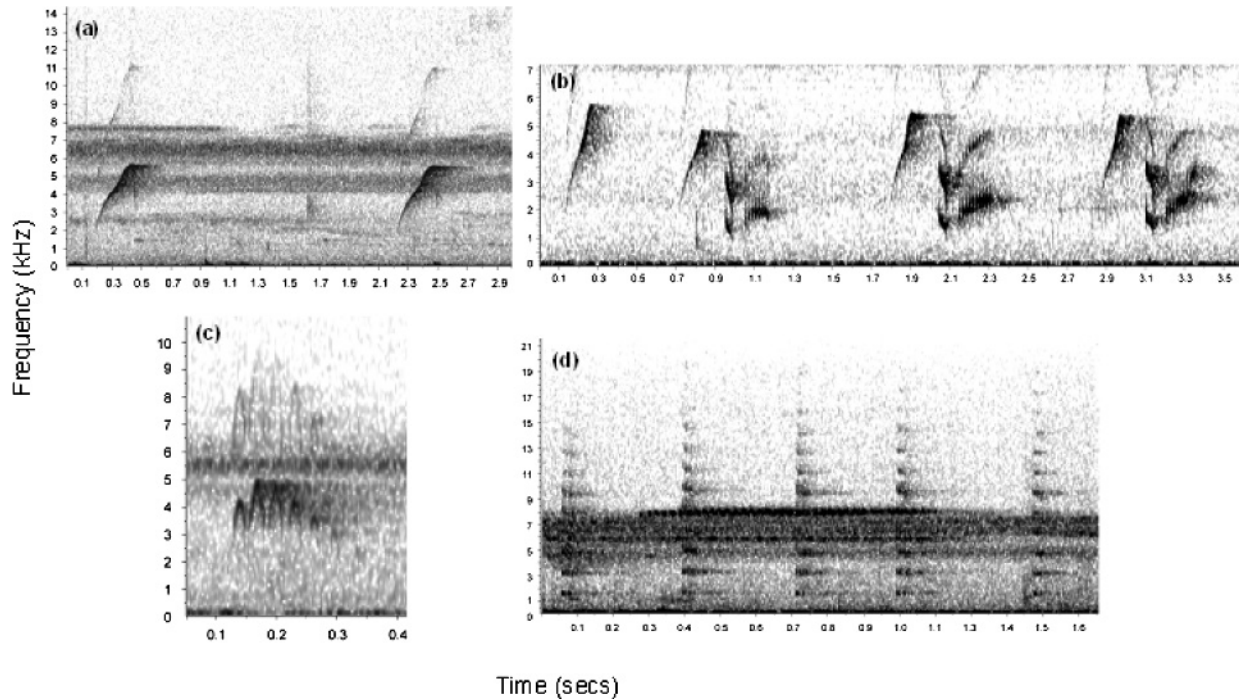


FIGURE 2. Sound spectrograms of vocalizations given by male Blue-crowned Manakins (*Lepidothrix coronata*) in eastern Ecuador. (a) Two *sweep* calls; (b) a series of three *chi-wrr* calls preceded by one *sweep* call; (c) *preew* call; (d) *pee* calls. Spectrograms were produced with a sample rate of 44.1 kHz and a 517-point (a, b) or 301-point (c, d) fast Fourier transform.

“Sweep” call or whistle (Fig. 2a, b). Contact call used by males and females of all ages. Territorial males give this whistle when vocalizing alone from song perches, while foraging, during interactions with other males or females, or during some display behaviors (see below). Soft *sweep* whistles are used by females and fledglings during foraging and by females when visiting males’ territories. The call is given as a single note or in bouts with a variable number of repetitions and is often given by males as an introduction to a bout of *chi-wrr* calls (below). It consists of a single high-pitched note lasting $0.23 (\pm 0.07)$ sec and ascending from $2.8 (\pm 0.5)$ to $5.7 (\pm 0.2)$ kHz. Territorial males gave this call during 87% of the 10-min observation blocks, at an average rate of 3.0 ± 2.8 calls min^{-1} .

“Chi-wrr” call (Fig. 2b). Main advertisement call used by territorial males; serves in territory defense and long-distance communication. It is given from song perches by males of all ages but not by females, as single notes or in series of up to five or six repetitions, often preceded by a *sweep* whistle. It consists of three parts; the first is a shorter, lower-pitched version of the *sweep* whistle, ascending from $3.0 (\pm 0.3)$ to $5.0 (\pm 0.4)$ kHz in $0.13 (\pm 0.04)$ sec. The second part is a short (0.06 ± 0.01 sec), descending note composed of three stacked harmonics, at approximately 1.4, 2.8, and 4.1 kHz; this notes ranges in frequency from $1.0 (\pm 0.1)$ to $4.6 (\pm 0.4)$ kHz. The last part of the call is a harsh, slightly ascending note composed of two harmonics centered on 2.0 and 3.9 kHz. This third part

lasts $0.20 (\pm 0.03)$ sec and spans frequencies from $1.3 (\pm 0.2)$ to $4.2 (\pm 0.3)$ kHz. The complete call lasts $0.45 (\pm 0.04)$ sec, and repetitions within a bout are separated by $0.75 (\pm 0.39)$ sec. Territorial males gave this call during 93% of the 10-min observations, at an average rate of 6.8 ± 3.8 calls min^{-1} .

“Preew” call (Fig. 2c). Only males were observed making this call, during interactions with other males or females entering their territories. This seems to be the same call Snow (2004) described as *“prrrreew”* for *L. coronata* and Skutch (1969) described as *“p’rrr”* for *L. coronata velutina* in Central America. It was usually associated with some display behaviors, in particular *wing-flicks*, *perch-to-perch chases*, *to-and-fro flights*, and *whirring to-and-fro flights* (see below). It is composed of four or five rapid oscillations between 3.1 and 6 kHz, with a total duration of 0.11–0.14 sec (I recorded this call from only three birds so present ranges rather than mean \pm SD). *Preew* is a relatively infrequent call noted in only 2% of the observation blocks, during which it was given at a rate of 4.9 ± 4.4 calls min^{-1} .

“Pee” call (Fig. 2d). This call is apparently given only by males during display. Although it was given relatively frequently (11% of the observation blocks), it is inconspicuous, and males were usually secretive when emitting it. Therefore I saw birds emitting this call on only a few occasions, when males were seen close to the ground but not necessarily at the display court. This call was also heard during the single copulation observed, during simulated copulations, and simultaneously

with some of the display behaviors (see below). It is given in bouts of one to ten repetitions, at a rate of 3.9 ± 4.3 calls min^{-1} . In the single recording obtained the series consists of flat notes of broad range with multiple (~10) harmonics between 1.5 and 15 kHz and lasting 0.03–0.06 sec.

DISPLAY BEHAVIORS

I identified in male courtship displays 11 behavioral elements, six of which are aerial displays and five are perched displays. All displays were observed exclusively at leks. These displays can be tentatively categorized in terms of the social context in which they are used: *Advertisement displays* (A) are performed aerially or by the perched bird outside the display court. They are not directly involved in copulation but can be involved in signaling toward other males or females and can be followed by courtship displays. *Courtship displays* (C) are part of the ritualized courtship repertoire given specifically at the dance court. They are often but not always performed in the presence of a female and can lead to copulation; males also engage in these displays in the absence of a visiting female, usually solitarily but sometimes together with juvenile males, during “practice displays.” Finally, *interactive displays* (I) are performed during male–male interactions, such as chases and displays by a perched group; they seem to have an intrasexual rather than courtship context. Some of the behavioral elements described below are used in more than one of the above contexts.

Wing-flicking (contexts A and I). While perched, the bird rapidly opens and closes the wings once, usually emitting a *preew* call. This display was used mostly during interactions with other males or females that entered the territory, in both aggressive and nonaggressive situations. It was usually given immediately after landing during *to-and-fro flights* and *high perch-to-perch flights* (see below).

To-and-fro flights (A). Series of flights back and forth between two horizontal perches located at the same level (2–4 m high) and separated by ≤ 1 m; immediately after taking off, the bird executes a 180° turn in the air and flies downward then upward in a U-shaped trajectory, landing on the second perch and facing away from the initial perch. Then the bird repeats this movement, returning to the first perch, again facing the opposite direction. This movement can be repeated several times, with *swee* or *preew* calls given at landing.

High perch-to-perch flights (A, I). Fast flights during which the bird moves continuously across the territory, darting among several horizontal perches separated by several meters and located between 5 and 10 m above the ground. Flights are usually shaped as a shallow S in reverse, with a slight downward and then upward trajectory. *Wing-flicks* are often given at landing, accompanied by *preew* or *swee* calls. This behavior was usually used during group chases among males, in which one bird left a perch immediately after the second one landed on it, or during individual displays by the

resident male upon arrival of another male or female at his territory.

Low perch-to-perch flights (C, I). Series of fast, short flights among three to five perches ≤ 1 m apart, similar to the previous display but performed much closer to the ground (at ~1.5 m or lower) and in a straighter trajectory than the shallow S-flights described above. This behavior was performed during the courtship displays given at the dance court, among mostly vertical but also horizontal twigs. When using vertical perches, the bird landed sideways and with the body in a vertical position. Occasionally, territorial males engaged in this behavior together with a visiting female or juvenile male, with both birds crossing each other in mid-flight.

About-face (A, C, I). Facing forward from a horizontal perch, the bird quickly turns 180° in place to face the opposite direction. It may be given in conjunction with *to-and-fro flights* and *wing-flicks* at perches 3–4 m high (context A) or at the dance court in conjunction with *low perch-to-perch flights*, *whirring to-and-fro flights*, and *bows* (context C). On one occasion, I observed an *about-face* with the body in a horizontal position, parallel to the ground; more observations are necessary to clarify if this behavior constitutes a separate stereotyped display element.

Frenzied flutter flight (A, C, I). A brief fluttering flight in which the bird hovers briefly in mid-air above the display perch. In another version, the bird simulates a copulation by hovering over a leaf and touching it with its cloaca, sometimes emitting a series of *pee* calls. This display was used in various contexts. In context A, the bird called from a song perch before executing an arc-shaped flight up and forward. At the apex of this trajectory, the bird stopped briefly in mid-air while fluttering its wings as if catching an insect, then returned down to the same perch or flew to a perch in front of the first one. In context C, this behavior was used during courtship displays at the dance court. The male jumped straight up from a horizontal perch close to the ground and stopped briefly in mid-air, fluttering its wings, emitting one *pee* call at the highest point of the flight, before landing back on the initial perch. Alternatively, the male appeared to simulate a copulation by hovering over a leaf between bouts of *whirring to-and-fro flights*. In a third context (I), this behavior was used during chases among males, which fluttered briefly over a leaf before resuming the chase.

Whirring to-and-fro flights (C). This behavior is performed close to the ground (< 1.5 m high) on the dance court during courtship display. The male performs a series of fast flights with circular trajectories, executing rapid perch changes among three to five vertical twigs with rapid, fluttering wing beats and landing sideways with the body held vertically. During flight, the body is hunched with the head and tail slightly lowered. At distance, the blue crown gives the appearance of a large blue *Morpho* butterfly. The bird is silent during flight, but it may emit *pee*, *swee*, or *preew* calls

upon landing. During very energetic displays, the male hovers in mid-air for a couple of seconds before landing. Each bout of flights that constitutes this display is short (5–45 sec), and up to eight bouts were recorded within 1 hr. Along with *low perch-to-perch flights*, this behavior was the most frequently observed, and probably the most energy-consuming, during courtship display.

Butterfly flight (I). A slow flight between perches with deep, exaggerated wing beats. It is mostly used in *butterfly chase displays*, when two or three males chase each other in slow, butterfly-like, up-and-down flights with deep wing beats; the bird reaches the perch in a circular trajectory, with the wings spread open and not flapping, as if soaring.

Side-to-side bowing display (C, I). While perched on a horizontal branch, the bird stretches its neck out, bends its body slightly forward, and, without moving its feet, turns its body about 45° first to one side and then to the other. Used during displays for females at the court and during group displays among perched males.

Side-to-side jump display (I). While perched on a horizontal perch and maintaining an erect posture, the bird makes a short hop to the side, without opening its wings. An *about-face* is sometimes executed during the hop, with the bird landing facing the opposite direction. This display was used during group displays by perched males.

Vertical wing display (I, C?). This behavior was observed only twice, but it is included here because it is part of the ritualized repertoire of other manakins (e.g., Castro-Astor et al. 2004), and additional observations may show it to be part of that of *L. coronata* also. From a horizontal perch, the bird raises both wings above its head, sometimes making a short jump upward simultaneously; the wing tips do not touch. On the first occasion I observed it, this display was given by an immature male displaying with a male in definitive plumage when both males were performing *low perch-to-perch flights* at the court of the resident adult male. When the adult male perched on a higher branch outside the court and started calling, the green male continued with the display, performing *low perch-to-perch* and *whirring to-and-fro flights* at the court. The green male then executed the vertical wing display, making a short upward jump and raising both wings while emitting a *pee* call. On the second occasion, two adult males were engaged in a chase when one of them perched and raised its wings overhead without jumping. Because I observed this display at least once during a “practice display” at a court, it is possibly involved in courtship. This could not be confirmed, however, because the two occasions were during male–male interactions.

MALE–FEMALE INTERACTIONS

Females interacted with males in definitive and predefinitive plumage during visits to leks, during which the females were invariably unaccompanied. At leks, it was usually

possible to distinguish between females and juvenile males by the behavior of the visiting bird. Juvenile males are usually more conspicuous than females, moving and vocalizing actively, and often emitting *chi-wrr* calls (not used by females) and executing ritualized display behaviors in the company of the territorial male or alone. Visiting females are usually more inconspicuous, remaining silent or vocalizing with soft *swee* whistles, and their presence often prompts territorial males to start displaying immediately. Usually I first noticed them when the resident male suddenly changed behavior (e.g., from being perched, silently or calling) and initiated *high perch-to-perch flights* across the territory, *flicking wings* at landing, and emitting *swee* and *preew* calls frenetically. After a few minutes, the male confines its flights to the area directly above the display court, now flying lower (1–2 m above the ground). Alternatively, the male simply perches above the display court, whistling and flicking its wings. With these behaviors, the male may be signaling the location of the court to the female in an attempt to attract her to that area. If the female flies down to the court, both birds may engage in *low perch-to-perch flights* at the court, <1 m above the ground, crossing paths in mid-air; alternatively, the female may perch unmoving or changing perches only occasionally while the male continues displaying. In the usual sequence of events, the male goes on to perform *whirring to-and-fro flights* among vertical perches in the display court while the female perches low in the court and sometimes emits soft *swee* whistles.

I observed 12 visits by females, four between 07:10 and 08:40, eight between 14:30 and 15:50. Disruption by other males was never observed during females’ visits. Only one of the observed visits ended in copulation. In this case, the male performed *whirring to-and-fro flights* while the female was perched at the court on a horizontal branch ~20 cm above ground; after one of the flights, instead of landing on a perch, the male alighted upon the female, hovering over her during a brief copulation while emitting *pee* calls, after which he resumed the whirring flights. Within <1 min, the male copulated with the female two more times, performing whirring flights between each copulation, after which the female flew away. After the departure of the female, the male gave a few *swee* whistles while perched at the court followed by several minutes of silence, after which he started singing actively from a higher song perch.

MALE–MALE INTERACTIONS

Interactions between males in definitive, predefinitive, and juvenile plumage are relatively frequent and appear to be nonaggressive for most part. The main types of male–male interactions observed were temporary associations between territorial and nonterritorial juvenile males, chases, and group perched displays.

Interactions between territorial and juvenile males. Green juvenile males do not hold stable territories. Although

they sometimes hold loose territories on the periphery of leks for short periods during the breeding season, their presence on these territories is not predictable. Juvenile males were frequently observed associating with territorial males. Usually, such associations seem to be directed toward a specific territorial male and may last several hours during a day and several days in a row. Juveniles are usually tolerated by territorial males and not chased away. While on the territory, juvenile males usually vocalize actively, emitting *chi-wrr* and *swee* calls from song perches, and practice courtship displays at the dance court, alone or together with the resident male. Both classes of males also frequently engage in chases (below).

Chases. Chases are interactive displays during which two or three birds fly after each other. They usually take place within a particular male's territory, but birds may move between territories during a chase. A male seems to have non-aggressive control over a chase in its territory: as soon as the territory holder lands on a song perch and starts emitting *chi-wrr* calls, the other interacting birds usually disperse. Chases usually take place ≥ 6 m above the ground, but birds occasionally come closer to the ground. Flights can be slow *butterfly flights* or faster *high perch-to-perch flights*. During these interactions, the birds remain mostly silent or emit *preew* calls, frequently making *wing flicks* at landing. Chases among territorial males belonging to the same lek are frequent and often also involve green-plumaged birds. These green birds are mostly likely males; in several instances this was confirmed either because they started emitting *chi-wrr* calls or via molecular sex determination in the laboratory. However, it is plausible that females were involved in these chases as well.

All observed chases were apparently nonaggressive, with one notable exception. An interaction between two males in definitive plumage had begun as a series of apparently nonaggressive chases when the visiting male started emitting *chi-wrr* calls and flicking its wings vigorously at the center of the territory. When chased away by the resident male, this visiting male remained in the territory, flying in small circles, with repeated perching and singing. During the chase, the resident male flicked its wings vigorously at landing but remained silent. The chases escalated in intensity, becoming very fast, and the territorial male nearly hit the intruder in mid-air on a few occasions. This aggressive chasing lasted at least 3 hr on this day and was again observed on my next visit to the territory 3 days later. I interpret this protracted, aggressive interaction as an attempt by the visiting male to take over the territory of the resident male.

Group perched displays. Perched displays involving more than one male are infrequent but potentially important components of the display repertoire of *L. coronata*. I observed the following sequence of displays between two adult males with contiguous territories within a lek. The sequence began with each male singing on its own territory. Male 1 (the resident male on the focal territory) began

performing *high perch-to-perch flights* (~5 m above the ground) with *about-faces* when landing on the corner of its territory abutting the territory of male 2. Male 2 flew into the territory of male 1, landing beside male 1 on a horizontal branch. One male (unclear which one) performed *about-faces* and *wing-flicks* while the other remained still beside the displaying male. Both males then flew straight up on an intertwined spiral trajectory, rising 1.5–2 m above the perch before separating and flying down in opposite directions. Male 2 returned to the perch and, while alone, for a few minutes performed *wing-flicks*, *about-faces*, including some with a horizontal posture, *side-to-side bowing displays*, *side-to-side jumps*, and *perch-to-perch flights* between two perches. At this point, male 1 landed beside male 2 and, for about 4 min, remained completely still while male 2 engaged in short *side-jumps* toward and away from male 1, along with *about-faces* and *wing-flicks*. Finally, both males engaged in *perch-to-perch flights* 2–3 m above the ground for a few minutes, after which male 2 flew back to its territory. During the entire sequence, both birds were completely silent.

DISCUSSION

Despite its wide neotropical distribution and high local densities, *Lepidothrix coronata* remains, along with the other seven species in the genus, one of the manakins least known behaviorally. Two short accounts published for Central American populations (Skutch 1969, Prum 1990) suggest a display repertoire smaller than that of other manakins. My study, based on more extensive observations in eastern Ecuador, contributes significantly to our knowledge of the lek dynamics and behavior of this species and reveals a display repertoire more diverse than previously recognized. Prum (1990) accounted for only three of the eleven displays I describe (*about-face*, *to-and-fro flight*, and *whirring to-and-fro flight*), while Skutch (1969) had previously identified other two (*wing-flicks* and *high/low perch-to-perch flights*). Furthermore, the geographical variation in plumage and vocalizations among subspecies of *L. coronata* suggests that behavior may vary geographically as well (e.g., Théry 1990), revealing additional breadth of this species' behavioral repertoire.

SPATIAL STRUCTURE OF LEKS AND TERRITORIES

The spatial structure of leks and territories of *L. coronata* in the Ecuadorian Amazon is in general agreement with observations made in Costa Rica by Skutch (1969), who described two "dispersed" leks containing three and seven territories, with males separated by 20–30 m from the nearest neighbor and holding singing perches located 1.5–9 m (but mostly 3–6 m) above the ground. One potential difference between these populations may be in degree of territoriality. Whereas in Costa Rica Skutch described territories as poorly defined, in the Ecuadorian population territory boundaries were well

defined and vigorously defended, especially along the contact zones between territories, even though visits by lek mates or nonterritorial males to established territories were relatively frequent. Within a territory, the display court of *L. coronata* resembles that of *L. serena* (Prum 1985, Théry 1990), “a loosely organized court near the ground composed of a few vertical and horizontal perches but without cleared ground” (Prum 1990).

DISPLAY REPERTOIRE OF *LEPIDOTHRIX CORONATA*

Although my observations substantially broaden the display repertoire of *L. coronata*, they do not reveal display movements unique to this species, whose repertoire still remains one of the least derived within the family (Prum 1990). *Wing flicks* are also present in the repertoire of *L. serena* (Prum 1985), the *erythrocephala* clade (which includes *Pipra erythrocephala*, *P. rubrocapilla*, *P. chloromeros*, *P. mentalis*, and *P. cornuta*; Lill 1976, Tello 2001), and maybe *Chiroxiphia pareola* (Snow 1963a), while in *L. isidorei* a display similar to *wing-flicks* is given in a chin-down posture and with shivering wings instead of a single fast flick of the wings (D. Calderón-Franco and M. Anciães, pers. comm.). *To-and-fro flights*, sometimes referred to as “darting back-and-forth flights,” are performed by *P. aureola* (Snow 1963b), the *erythrocephala* clade (Skutch 1969, Lill 1976, Tello 2001, Castro-Astor et al. 2004), *Dixiphia pipra* (Snow 1961, Castro-Astor et al. 2007), *Machaeropterus deliciosus*, *Corapipo gutturalis*, and *L. serena* (Prum 1990); from these accounts, however, it is unclear if the clear U-shaped trajectory of the display flight of *L. coronata* is also part of these other species’ repertoires. *About-face* is another common display, performed by *L. serena* (Prum 1990), the *erythrocephala* clade (Skutch 1969, Lill 1976, Tello 2001, Castro-Astor et al. 2004), *M. deliciosus* (Bostwick 2000), *D. pipra* (Snow 1961, Castro-Astor et al. 2007), and *C. gutturalis* (Théry 1990). *Lepidothrix coronata* performs *about-faces* mostly in an erect posture but was also observed performing them once in a horizontal posture, as does *L. isidorei* (repeated a few times consecutively, D. Calderón-Franco and M. Anciães, pers. comm.) and two species in the *erythrocephala* clade, *P. rubrocapilla* (with wings spread horizontally; Castro-Astor et al. 2004), and *P. mentalis* (accompanied by wing flapping; Skutch 1969). *Frenzied flutter flights*, which may have evolved as simulated copulations, are relatively common as well, having been reported for the *erythrocephala* clade (Lill 1976, Prum 1990, Tello 2001, Castro-Astor et al. 2004) and the *aureola* clade (which includes *P. aureola*, *P. fasciicauda*, and *P. filicauda*; Robbins 1983, Prum 1990). *Butterfly flights/chases*, also frequent in the repertoire of several manakins, are hypothesized to have evolved independently at least four times (Prum 1990). The apparently less frequent *low/high perch-to-perch flights* are also performed by *L. serena* (Prum 1985, Théry 1990) and may be equivalent to the “rapid flights” made by *Corapipo leucorrhoea* (Rosselli

et al. 2002). Finally, the *vertical wing display* is also performed by *P. rubrocapilla* (Castro-Astor et al. 2004).

In other cases, elements similar to those performed by *L. coronata* occur in the repertoire of other manakins with slight modifications. The *side-to-side jump* of *L. coronata* resembles the display of the same name found in the *aureola* clade (Schwartz and Snow 1978, Robbins 1983, Prum 1990) with the difference that *L. coronata* does not assume a stereotyped hunched posture. Similarly, *D. pipra* performs short and long side jumps with an erect posture (Castro-Astor et al. 2007). The *side-to-side bowing* display of *L. coronata* resembles the one performed by *Masius chrysopterus* (Prum and Johnson 1987), with the difference that *L. coronata* does not assume the stereotyped posture of *Masius* with the plumage fluffed out and tail cocked. Finally, other manakins (e.g., *Manacus*) have displays during which males move between vertical perches close to the ground, but the *whirring to-and-fro-flight* may be unique to *Lepidothrix* spp., as previously suggested by Prum (1990). This behavior was observed also in *L. serena* by Prum (1990) and in *L. isidorei* by D. Calderón-Franco and M. Anciães (pers. comm.).

COORDINATED DISPLAY AMONG MALES

Coordinated display, in which two or more males engage in interactive, synchronized displays, is known in 12 of 27 manakin species for which information is available. It seems to have multiple independent origins within the family (Prum 1994). Prum (1994) described the coordinated display of *L. coronata* and *L. serena* as simple, i.e., synchronized interactive performances of solitary display elements performed by transitory pairs of males; this simple display differs from complex coordinated displays in which novel elements not performed during solitary displays are introduced. My observations confirm this distinction, to the extent that the same elements used during solitary displays are used during aerial group displays (chases with *perch-to-perch* or *butterfly flights*, with *wing-flicks* at landing). While this was generally true also for a perched display involving two males (in which *low perch-to-perch flights*, *about-faces*, *side-to-side bowing* were used), it is unclear if this was truly a coordinated display, since only one of the males displayed while the other remained still. Yet it is interesting to note that this was the only context in which I observed the *side-jump* display. More extensive observations should clarify whether this is a movement directed exclusively to other males.

As in *L. serena* (Prum 1985, Théry 1990), in *L. coronata* coordinated displays take place within males’ territories and involve the resident male and one or two other males in adult or juvenile plumage. These associations are not permanent, although these interactions frequently involve neighboring territorial males belonging to the same lek or else a territorial male and juvenile that repeatedly visits the territory and may establish a “loose” territory on its periphery. In most cases,

these group displays did not involve overtly aggressive interactions among the males. These observations support Prum's (1985) and Théry's (1990) claim that in *Lepidothrix* coordinated displays serve more to establish male dominance hierarchies than to attract mates (in contrast to other manakins such as *Chiroxiphia*, Foster 1981). However, coordinated displays could also establish and reinforce social bonds among males that might play a role in information sharing (e.g., about food sources) and, especially for juvenile males, perfect elements of display.

ACKNOWLEDGMENTS

I thank Bette Loiselle, John Blake, Patricia Parker, Thomas Ryder, Wendy Tori, and José Hidalgo for their invaluable contribution to the completion of this study. Jaime Guerra, Consuelo and David Romo, Kelly Swing, and all the staff at TBS made my research in Ecuador possible. Marina Anciães and Diego Calderón-Franco kindly shared their observations on *Lepidothrix isidorei*. I worked under permission no. 13-IC-FAU-DFN granted by the Ministry of the Environment of Ecuador and Institutional Animal Care and Use Committee protocol no. 5-12-20. Bart Kensinger, Ken Hiser, Franklin Narvaes, and José Grefa assisted with data collection. This work was funded by the National Science Foundation (IBN-0235141, DEB-0304909), National Geographic Society (7113-01), University of Missouri–St. Louis, International Center for Tropical Ecology, and Idea Wild. I was supported by a doctoral scholarship from CAPES (Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), a research assistantship from the National Science Foundation, a Raven fellowship and a teaching assistantship from the University of Missouri–St. Louis. Marcos Gridi-Papp aided with spectrograms' preparation. Richard Prum, Marina Anciães, Jordan Karubian, and an anonymous reviewer provided valuable comments.

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