

## LEKING BEHAVIOR OF THE ROUND-TAILED MANAKIN<sup>1</sup>

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**Abstract.** Along the Rio Manu in southeastern Peru, Round-tailed Manakins (*Pipra chloromeros*) breed mainly from August to November. Male *P. chloromeros* have a dispersed lek breeding system, with each lek composed of two to five territorial males. Sites used by males for display had significantly higher densities of shrubs, vines, and small trees than did non-display sites. Interlek distances ranged from 220 to 1000 m. Within leks, most males occupied territories within auditory range, but not visual range. Distance to the closest neighbor's display perch varied from 8 to 87 m. Males vigorously defended territories that ranged from 20 to 50 m in diameter. Males progress in social status within the lek (from immature to non-territorial adult to territorial adult). Territorial adult males were always dominant to males of the other two categories. Territorial males engaged in daily ritualized encounters at the borders of their territories. Encounters involved slow, coordinated displays reminiscent of those performed toward females. Such interactions may help maintain dominance relationships within the lek, but an analysis of interaction outcomes failed to show clear dominance relationships among males. Female visitation was most frequent in early afternoon, during males' maximum territory attendance and display activity. Lekking *P. chloromeros* employ ten display elements, six vocalizations, and one mechanical noise. One display element has not been observed in any other species of *Pipra*. The displays and sounds in the *P. erythrocephala* clade are compared from the perspective of understanding the evolution of display behavior in this group.

**Key words:** courtship, display, lek, manakins, *Pipra chloromeros*, social organization, song.

### El Comportamiento de Lek del Saltarín de Cola Redonda

**Resumen.** El comportamiento de lek del Saltarín de Cola Redonda (*Pipra chloromeros*) fue estudiado en el Río Manu, sudeste del Perú. Esta especie tiene un sistema de leks disperso, con leks compuestos de 2 a 5 machos territoriales. Las áreas de despliegue tuvieron densidades significativamente altas de arbustos, lianas y árboles pequeños, en comparación con áreas sin leks. La distancia entre leks varió de 220 a 1000 m. Dentro de los leks, los machos defendieron territorios de 20 a 50 m de diámetro. La distancia entre territorios varió de 8 a 87 m. Los machos experimentan una progresión en status social dentro del lek (machos inmaduros, machos adultos no-territoriales y machos adultos territoriales). Los machos territoriales mantuvieron encuentros diarios altamente ritualizados en los límites de sus territorios. Estos encuentros incluyeron elementos del despliegue de cortejo, aunque de más baja intensidad. Estos encuentros servirían para mantener las jerarquías sociales dentro del lek. Sin embargo, un análisis de los resultados de estas interacciones no mostró un patrón claro de dominancia. Las visitas de las hembras coincidieron con las horas de máxima atención del territorio y el pico de actividad de despliegue. El repertorio de despliegue de esta especie incluyó diez elementos de despliegue, seis vocalizaciones y un sonido mecánico. Uno de estos elementos no ha sido previamente descrito para ninguna otra especie de *Pipra*. Los despliegues, vocalizaciones y sonidos mecánicos presentes en el clado de *P. erythrocephala* son comparados con la perspectiva de entender la evolución del comportamiento de despliegue en este grupo.

### INTRODUCTION

Manakins (Pipridae) are among the most colorful small passerine birds of the Neotropics, with

the majority of species exhibiting marked sexual dimorphism, elaborate courtship displays, and lek breeding systems (Snow 1963a, Sick 1967, Prum 1990, 1994). The social organization of leks is of particular interest to ethologists because lekking so strikingly epitomizes the conflict between advantages (e.g., more females attracted, decreased predation risk) and disadvantages (heightened competition and aggression)

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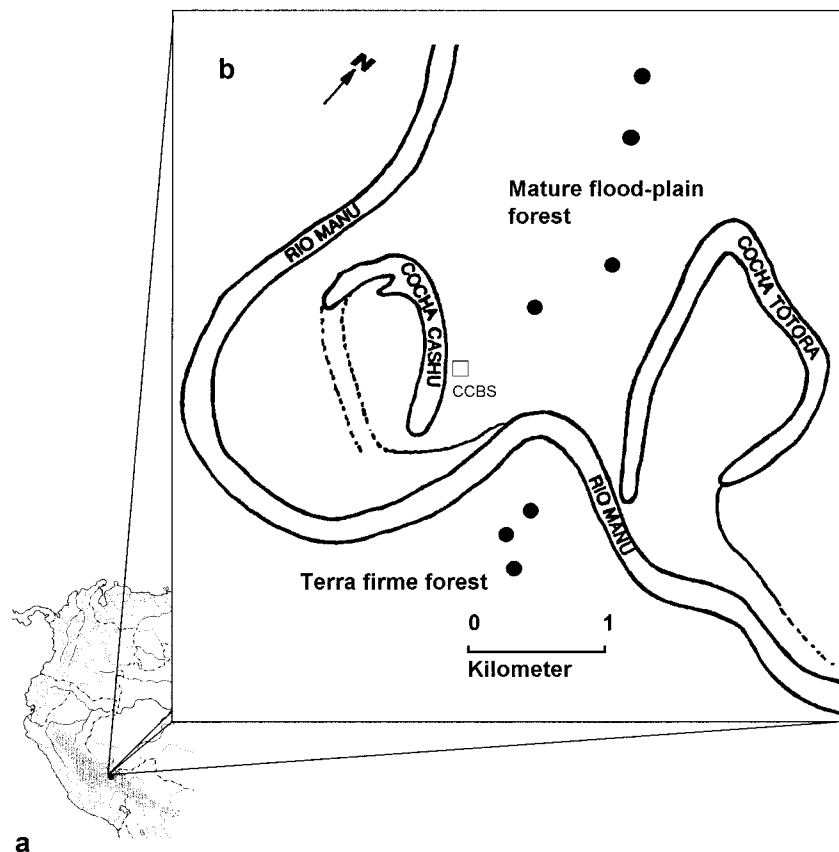


FIGURE 1. (a) Geographic distribution of *Pipra chloromeros* and location of the study site, Cocha Cashu Biological Station (CCBS), on the Rio Manu, Peru (black dot). (b) Distribution of *Pipra chloromeros* leks (black dots) at mature floodplain and terra firme forest around CCBS.

inherent in a highly social mode of life (Alexander 1974). A presumed function of social organization within such species is resolution of this conflict through amelioration of the disadvantageous effects of social life. This is particularly true of tropical lekking species with extended breeding seasons, like those of *Pipra* spp., in which males spend most of their waking adult life very close to other males at leks (Snow 1962, Lill 1976, Robbins 1985).

Prum's (1990, 1992, 1994) comparative studies of the manakins demonstrate that lek breeding evolved early in the Pipridae, and that many aspects of the display and reproductive behavior vary phylogenetically among closely related genera and species of manakins. Although something is known about the courtship behavior of more than half of the family's 40 species, some have not yet been studied. Additional work

on the poorly known species is essential to advancing our understanding of the evolution of behavior in the family (Prum 1996).

In this study, I report on lekking behavior of the Round-tailed Manakin (*Pipra chloromeros*). Our understanding of behavior in this manakin is limited to some notes of Niethammer (1956) and unpublished observations cited in Prum (1990). *Pipra chloromeros* is found in humid forest, both in upper tropical and lower subtropical zones (300–1400 m) from eastern Peru (Dpto. Amazonas and San Martin) to northern Bolivia (Dptos. La Paz, Cochabamba, and western Santa Cruz) (Snow 1979, Ridgely and Tudor 1994; Fig. 1a). Based on morphology and zoogeography, *P. chloromeros* is closely related to the Scarlet-horned (*P. cornuta*), Red-capped (*P. mentalis*), Red-headed (*P. rubrocapilla*), and Golden-headed (*P. erythrocephala*) Manakins

(Haffer 1970, Prum 1990, 1992). These five species comprise the *P. erythrocephala* clade (Prum 1992).

My goal in this study was to document the social and reproductive behavior of this poorly known species. My objectives were (1) to determine abundance, spatial distribution, and social structure of *P. chloromeros* leks; (2) to describe and quantify characteristics of the habitat selected by males for display sites; (3) to describe social organization and courtship behavior; and (4) to compare the display behavior among members of the *P. erythrocephala* clade.

## METHODS

### STUDY SITE

Observations were conducted in an undisturbed lowland wet forest at Cocha Cashu Biological Station (11°54'S, 71°18'W, elevation ca. 400 m, Fig. 1a), Manu National Park, Department of Madre de Dios, southeastern Peru. Mean temperature at the station is 23°C to 24°C, and rainfall averages about 2000 mm annually (Terborgh et al. 1990). Rainfall is concentrated during a five-month rainy season extending from late November to early May. On average, less than 100 mm of rain falls during the dry season.

The sinuous meanderings of the Manu River transform the landscape both spatially and temporally. At each bend, forest on the outer side of the river is annually undermined and carried away, while on the inside shore, new land is laid down in the form of broad beaches (Terborgh 1983). As a result of this riverine dynamic, a narrow mosaic of successional forest types occurs in the inside shore, producing distinctive vegetation zones. Forests in the vicinity of Cocha Cashu fall into two broad categories, floodplain (near the inside shore on flat terrain, seasonally flooded) and terra firme (far from the inside shore on hilly terrain, never flooded). More complete descriptions of the area and its ecology are presented by Terborgh (1983), Foster et al. (1986), and Gentry and Terborgh (1990).

### DATA COLLECTION

Observations were made during four field seasons: August to November 1989, August to September 1990, August to November 1992, and August to December 1994. To determine patterns of distribution and abundance of *P. chloromeros*, I conducted censuses along a 50-km

trail system located in floodplain and terra firme forests using the spot-mapping method (Ken-deigh 1944). Manakins were counted within a 100-m-wide band centered on the trail. Positions of singing males were estimated, using a compass, as the direction and straight-line distance from the nearest trail marker; markers were located at 25-m intervals on all trails. Mapping records of successive censuses along each transect produced clusters of points that were assumed to represent the locations of individual territories (courts) or clusters of males. I later visited these locations to determine whether a lek was present. I completed 210 hr of censuses in floodplain forest and 130 hr in terra firme forest between 1989 and 1994. Censuses covered a total area of approximately 7 km<sup>2</sup> in floodplain and 1 km<sup>2</sup> in terra firme forest. Censuses were conducted from 06:00 to 10:00 and from 12:00 to 15:00.

Interlek distance was measured as the distance from the center of one lek to the center of the nearest conspecific lek. Number of territorial males per lek and locations of adult male display courts were determined by direct observation. At some leks, where males were individually color-banded, I mapped the locations of all the perches used by each territorial male. Then, court size for each male was drawn on a map using the modified minimum-area polygon method (Harvey and Barbour 1965), and the area was measured using SigmaScan/Image measurement software (Jandel Scientific 1993).

Characteristics of the habitat used by *P. chloromeros* were quantified at six display sites in 1989 and two in 1994. Vegetation samples from control areas (13 randomly selected places within the same types of forests used by the manakins) were compared with samples made at the courts. Data from randomly selected control samples were provided by Dr. M. Foster (U.S. Geological Survey, Biological Resources Division, Washington, DC). The sampling method was a modification of the James and Shugart (1970) method of vegetation analysis. A circular plot of 11.3-m radius was located approximately at the center of the court or sample area. Two transects of 22.6-m length, oriented east-west and north-south, were established within each circle. In these transects, 10 and 11 points, respectively, were used to estimate relative vegetation cover (both ground and canopy) using a cardboard tube with two threads crossed over

one opening. These lines divided the field observed into four cells. At each point, the number of cells in which at least 50% of the area was covered by vegetation was recorded by looking straight up at the canopy and straight down at the ground. Density of woody shrubs and saplings (<7.5 cm diameter at breast height [dbh]) was measured by walking N-S and E-W transects with arms outstretched and counting all stems encountered, including woody vines and palms, (i.e., plants  $\geq 1.5$  m tall). Number of trees, including large palms, with dbh  $\geq 7.5$  cm was recorded for the entire sample circle; trees were assigned to size categories (7.5–10 cm; 10.1–12.5 cm; 12.6–15 cm; 15.1–20 cm; 20.1–25 cm; 25.1–55 cm; and >55 cm). Two-sample *t*-tests were used to evaluate differences between manakin display plots and randomly selected plots for each habitat variable separately (i.e., ground and canopy cover, density of shrubs with dbh < 7.5 cm, density of all trees with dbh  $\geq 7.5$  cm). Mann-Whitney *U*-tests were used when data did not meet an assumption of normality. Discriminant function analysis (DFA) was used to explore what combination of variables, if any, best distinguished habitats at manakin display and non-display sites.

Non-structured behavioral observations of *P. chloromeros* leks were made from 1989 to 1992. In 1994, behavior of territorial males at two leks was observed for a total of 360 hr using focal sampling (Altmann 1974). Every male was observed for an equal number of hours for a total of three days. Five periods of observation were distributed between 05:30 and 16:00 and lasted 2 hr (the first four periods), except the fifth period, which lasted for 1.5 hr. Within each period, I conducted focal observations of 3-min duration, at 15-min intervals, and recorded descriptions of the displays and behavior of adult males, immatures, and females; female visitations and copulations; calling activity (number of advertisement calls); display activity (number of flight displays); interactions with neighbors and non-territorial and juvenile males; and duration of territory absence. Young males were distinguished from females by their plumage (if molting into adult plumage), their behavior at the lek, and the reaction of territorial males when these individuals visited their courts. For all perches used by territorial males I recorded the following data: perch type, perch inclination (angle from horizontal), height, diameter, and

height of the nearest vegetation cover above the perch. I also recorded vocalizations and mechanical sounds associated with displays. Recordings were made with a Sony TCM-5000EV tape recorder and an MK67 unidirectional Sennheiser microphone. Spectrograms were prepared with Canary 1.2 song analyzer software (Charif et al. 1995). To facilitate comparisons, I have adopted, whenever possible, the terminology of Robbins (1983) and Prum (1990) to describe vocalizations and displays of *P. chloromeros* relative to those of other members of the genus. Display drawings were prepared by M. Skakuj using video, photos, sketches, and verbal descriptions.

At the two focal leks, court boundaries of individual territorial males were determined by mapping the locations of agonistic encounters between pairs of neighbors (Lill 1974, 1976) and by noting movements of territorial males during periods of observation. Dominance relationships were evaluated using data from the territorial encounters. I used number of approaches, withdrawals, and percentages of approaches causing withdrawals to test for differences in dominance relationships between interacting pairs. Dominant males were expected to approach more, withdraw less, and cause more withdrawals than subordinate males (Lill 1974, 1976). Data were compared using Mann-Whitney *U*-tests. Because foliage often obscured territorial encounters, the number observed was low. Thus, I chose to analyze dominance relationships only between pairs of adjacent territorial males with at least six encounters.

The effect of lek size (number of males) on female visitation, male success, and overall display behavior was evaluated using data from the two leks, which included two and five males, respectively. These leks were approximately 650 m apart in floodplain forest. Data on female visitation, number of observed copulations, visits of immatures, calling activity (number of vocalizations), display activity (number of flight displays), and number of boundary encounters between males recorded at these two leks were used in this comparison. For the purpose of these comparisons, lek totals and male averages, for these variables, were calculated ( $n = 3$ ). Data were compared using Mann-Whitney *U*-tests. Because of the small sample size (i.e., two leks) these analyses were primarily descriptive. Values presented are means  $\pm$  SE.

## RESULTS

### DISTRIBUTION AND ABUNDANCE OF LEKS

Leks of *P. chloromeros* were found in both mature floodplain ( $n = 4$ ) and terra firme forests ( $n = 3$ ) (Fig. 1b). Interlek distances ranged from 220 to 1000 m (mean =  $512 \pm 144$  m,  $n = 5$ ). Lek density in floodplain forest was lower ( $0.6$  leks  $\text{km}^{-2}$ ) than in terra firme forest ( $3$  leks  $\text{km}^{-2}$ ). In floodplain forest, two other manakin species, Band-tailed (*P. fasciicauda*) and Blue-crowned (*P. coronata*) Manakins, were more common than *P. chloromeros*.

As with other lekking birds, leks were persistent at particular sites across seasons (Lill 1976, Foster 1981, MacDonald 1990). When I ended my observations in 1994, at Cocha Cashu, two leks of *P. chloromeros* had persisted at the same sites for at least 5 years, and four at the same sites for at least 7 years.

### DISTRIBUTION OF MALE TERRITORIES AND DISPLAY SITES

Two to five *P. chloromeros* males occupied courts on each lek. Within leks, most males occupied courts within auditory range of each other, but some males used display perches close enough to also maintain visual contact. Distance to the closest neighbor display perch averaged  $30.5 \pm 12.8$  m ( $n = 6$ ). Defended territories ranged in size from 20 to 50 m estimated diameter (mean =  $25.1 \pm 3.0$  m,  $n = 7$ ). Territorial males gave frequent advertisement calls and aggressively excluded other males.

Individual males used between 8 and 26 different perches in their courts. Perches were always free of obstructing vegetation (twigs or foliage) for at least 0.5 m, leaving clear pathways in front of and behind the perch. Although located in areas with relatively open canopies, perches in general had thick vegetation overhead, which could provide protection against predation. Perches were mainly horizontal, ranging between 0.3 and 2.5 cm in diameter, and from 4 to 16 m above the ground. Average heights of perches varied significantly among males (ANOVA:  $F_{6,103} = 13.1$ ,  $P < 0.001$ ), but perch diameter was consistent among males (ANOVA:  $F_{6,103} = 1.7$ ,  $P > 0.05$ ). Each male court included one or two horizontal display perches, one to three accessory perches adjacent to the display perches, and from 5 to 19 advertising perches. Display perches varied from 0.5

to 1.3 cm in diameter (mean =  $0.9 \pm 0.1$  cm), and 8 to 16 m above the ground (mean =  $9.8 \pm 0.8$  m).

### CHARACTERISTICS OF THE HABITAT USED FOR DISPLAY SITES

Most leks were located in mature forest on flat terrain. Two leks in terra firme forests were located close to a moderately steep slope. The forest around leks was moderately open, with an average canopy height of 30 to 35 m. A few emergent canopy trees (e.g., *Dipteryx micrantha*, *Ficus* spp.) extended to ca. 45 m. Ground cover varied from bare to moderately covered with herbaceous growth. A nearly monotypic layer of ferns (*Tectaria incisa* var. *vivipara*) dominated the ground in some areas, whereas in other sites, ferns were replaced by short species of *Heliconia* (Terborgh 1983). The understory included many species of shrubs and treelets that produce red or dark purple berries eaten by the manakins (e.g., many species of *Psychotria*, *Miconia*, *Neea*, and *Ardisia*). In some areas of terra firme forest, the understory was dominated by dense patches of bamboo (*Guadua* sp.).

Univariate comparisons showed that sites used by *P. chloromeros* males for display had significantly higher densities of shrubs and treelets ( $<7.5$  cm dbh and  $\geq 1.5$  m tall), vines ( $<7.5$  cm dbh), and small trees (10.1–12.5 cm dbh) than did randomly selected non-display sites (Table 1). A DFA using these three variables was significant ( $P < 0.01$ ) and correctly classified 90.5% of the cases. Thus, both univariate and multivariate analyses demonstrate differences between display and non-display sites. These results suggest that sites used for displays are selected in part because of structural features of the vegetation, presumably the denser understory.

### DISPLAYS, VOCALIZATIONS, AND OTHER SOUNDS

The display repertoire of *P. chloromeros* includes ten display elements, six vocalizations, and one mechanical noise. The frequency of occurrence at which *P. chloromeros* males performed certain displays and sounds varied, but all males regularly performed a combination of certain behaviors (Table 2). I first describe the displays, and then the vocalizations and other sounds with which they are associated.

*Upright posture.* The male assumes a posture

TABLE 1. Mean  $\pm$  SE proportion of cover (%), densities (per 0.04 ha) of vegetation features, and canopy height (m) recorded at 8 *Pipra chloromeros* display sites and 13 non-display sites along the Manu river, Madre de Dios, Peru. \*  $P < 0.05$ ; \*\*  $P < 0.005$  (Mann-Whitney  $U$ -tests).

Variable	Display sites	Non-display sites
Percent cover		
Ground	44.0 $\pm$ 5.0	35.0 $\pm$ 3.0
Canopy	95.0 $\pm$ 1.0	97.0 $\pm$ 1.0
Shrubs (<7.5 cm dbh)	59.1 $\pm$ 5.1**	38.0 $\pm$ 4.0
Vines (<7.5 cm dbh)	34.3 $\pm$ 10.0*	8.6 $\pm$ 1.5
Trees ( $\geq$ 7.5 cm dbh)		
7.5–10 cm dbh	8.9 $\pm$ 1.2	9.5 $\pm$ 1.1
10.1–12.5 cm dbh	6.9 $\pm$ 0.7*	4.7 $\pm$ 0.5
12.6–15 cm dbh	3.9 $\pm$ 1.0	4.7 $\pm$ 0.7
15.1–20 cm dbh	4.6 $\pm$ 1.1	5.4 $\pm$ 0.7
20.1–25 cm dbh	2.6 $\pm$ 0.4	2.9 $\pm$ 0.6
25.1–55 cm dbh	2.6 $\pm$ 0.7	1.8 $\pm$ 0.3
>55 cm dbh	2.3 $\pm$ 0.5	2.4 $\pm$ 0.5
Canopy height <sup>a</sup>	14.0 $\pm$ 2.8	13.0 $\pm$ 0.6

<sup>a</sup> Represents the average height of all vegetation layers at each plot.

in which the head is held nearly vertical, with the bill pointed up. Males assume this posture during encounters at court boundaries. It is also the position assumed by the female when she arrives at the display perch and the male initiates courtship.

*About-face.* A male makes a rapid 180° turn in place on a single perch between to-and-fro flights. About-faces may be accompanied by a rapid flick of the wings (no mechanical noise involved). A slower version of this display also occurs during boundary encounters among territorial males.

*To-and-fro flight.* A male flies back and forth between his main perch and one or two adjacent accessory perches 50 to 100 cm away. The male does an about-face immediately after landing on a perch. A displaying male sometimes gives the main phrase of the advertisement call (see below) immediately after arriving at a perch. This is sometimes preceded by the introductory phrase, which is given in flight. Occasionally, males make a double-wing snap immediately after landing on the perch. Less frequently, this mechanical sound is performed simultaneously with an advertisement call after landing. To-and-fro flights were the most common displays performed by males at the leks (48.6% of all observed displays) and generally occurred when a

TABLE 2. Occurrence of displays, vocalizations, and other sounds at two *Pipra chloromeros* leks in 1994. Percentage occurrence of each display or display sound during focal samples was calculated separately by dividing the number of observations of each display or display sound by the total number of observations of all different types of displays (1055) or display sounds (3112), respectively.

Displays, vocalizations, and other sounds	Percentage of occurrence
Displays	
To-and-fro flight	48.6
Type I flight display <sup>a</sup>	13.1
Wing-flick + pivot	9.9
Backward slide	10.7
About face	8.9
Squat	7.1
Type II flight display <sup>a</sup>	1.3
Frenzied-flutter <sup>a</sup>	0.4
Side-to-side	<0.3
Upright posture	<0.3
Vocalizations and other sounds	
Advertisement call	79.4
Display call	15.0
Appeasement whistle	4.3
Double-wing snap	1.3

<sup>a</sup> Vocalizations associated with these displays were not included in the analysis.

female-plumaged bird (a female or a young male) visited a male's court. This display presumably functions to attract visiting birds to the display area.

*Squat.* This display resembles the display described by Lill (1976) for *P. erythrocephala*. The male crouches transversely on his perch with legs bent. He fans his tail (which enhances its roundness) and lowers his partially spread primaries, quivering them rapidly, while making rapid side-to-side jumps. Sometimes the display ends with a mechanical noise similar to the double-wing snap, a sound also produced by *P. mentalis* (pers. obs.), and *P. cornuta* (Natural Sound Archive recording 26161; R. Prum, personal recordings), but not as loud. I usually observed this display when the male was excited, as, for example, when a female was present at the display perch of another male, or when another male was present in his court. After the display, the male usually abandons the display perch and then returns with a flight display from one of the accessory perches.

*Wing-flick.* This display involves several rapid flicks of the wings (no mechanical noise in-

volved). Flicking generally alternates with pivots (rapid 45° turns in place on a single perch), although sometimes they are simultaneous (wing-flicks + pivots, see Backward slide). Wing-flicking is an element of both courtship displays and territorial interactions.

*Backward slide.* With the body oriented lengthwise along or nearly along the perch, tail elevated, legs stretched, body feathers elevated, and head lowered, a male takes short rapid steps backward for 15 to 30 cm along the display perch, giving the appearance of sliding quickly (Fig. 2a). At the end of the slide, one of the following behaviors occurs: (1) With the body still parallel to the perch, the male raises his tail and head, adopting a "U" posture for 2 to 3 sec (Fig. 2b). A soft *hick* sound (of unknown source) accompanies this movement; (2) The male wing-flicks + pivots on the perch, and then suddenly abandons the perch and returns with a flight display (see below); (3) With the body oriented almost perpendicular to the perch, the male spreads his wings horizontally for a moment, quivers them, and suddenly fans his slightly depressed tail (Fig. 2c–e), sometimes giving a display call (*Fi-cuac-cuac*). Less frequently, the male just spreads his wings for a moment without quivering; (4) The male vibrates his wings extremely rapidly as in the squatting display; or (5) The male makes an about-face and with the body parallel to the perch slides backward toward his starting location.

*Side-to-side slide.* With the body oriented perpendicular to the perch, the male takes very short steps (slides) back and forth for 5 to 10 cm. Side-to-side slides were seen only occasionally, during encounters between territorial males at their court boundaries.

*Type I flight display (Swoop-in flight display).* The male flies downward and then upward to a higher perch (12–15 m high), 15 to 20 m away from his display perch. After 2 to 3 sec, he returns to his display perch, flying rapidly and again tracing a horizontal S-pattern in flight (Fig. 3a). A Type I flight display call is usually given on landing (Fig. 4f). Immediately after perching, the male sometimes executes one or more backward slides (Fig. 3c) or squatting displays (Fig. 3b) before leaving the perch to repeat the display. Type I flight displays were mainly performed by males when females visited their territories, and, thus, constituted an important element of the courtship of this species (13.1%,

the second most common display in the *P. chloromeros* display repertoire).

*Type II flight display (Catapult-like flight).* This less frequently observed flight display (1.3%) may be primarily agonistic. I observed it mainly when juveniles or other bird species were present in the display area. As in the display described above, the male flies to his main perch or another higher perch 15 to 20 m away, and then flies rapidly downward, ending with an inverted "U" trajectory toward his main perch. Upon arriving at the perch, he vocalizes (Fig. 4g) or, less frequently, makes a buzzing noise (probably of mechanical origin, recordings are not available). As in *P. mentalis*, this buzzing noise is similar to the sound produced by jerking a piece of cloth between the hands (Skutch 1949, pers. obs.) but softer. In a few observations of this behavior, the male remained frozen for a few seconds after arriving on his display perch and then made about-faces, wing-flicks + pivots, and flight displays.

*Frenzied-flutter.* This display is a pseudo-copulation, in which the male performs a brief fluttering flight while hovering above the display perch or a nearby leaf and emitting the frenzied-flutter call. This display occurred generally when the male was highly excited (e.g., when an unreceptive female left the display perch).

*Advertisement call.* The typical advertisement call is a multisyllabic *Fui-ii-ii-i—chi-awaaak* that lasts for about 1.7 sec (Fig. 4a). It is homologous to calls described for *P. cornuta*, *P. mentalis*, *P. rubrocapilla*, and *P. erythrocephala* (Skutch 1949, Snow 1962, 1977, Sick 1967, Lill 1976). Introductory (IP) and main (MP) phrases are easily distinguished in the advertisement call. The MP is preceded by the IP in 43% of all advertisement calls. The IP never follows the MP and is rarely given alone. The IP consists of three to six short whistles that decrease in frequency from 4 to 2 kHz and last about 0.5 sec. The MP is the most frequently heard type of advertisement call at *P. chloromeros* leks (57%). This vocalization is a three-element call, *chi-awaaak*, that lasts for about 0.3 sec. The MP starts with a dominant frequency of about 7 kHz (first element), shifts downward to about 2 kHz (second element), and finishes with a buzzing sound (third element) at about 4 kHz. In general, advertisement calls are loud and can be heard up to 100 m away. These calls were rarely given when a female was on the lek and were never

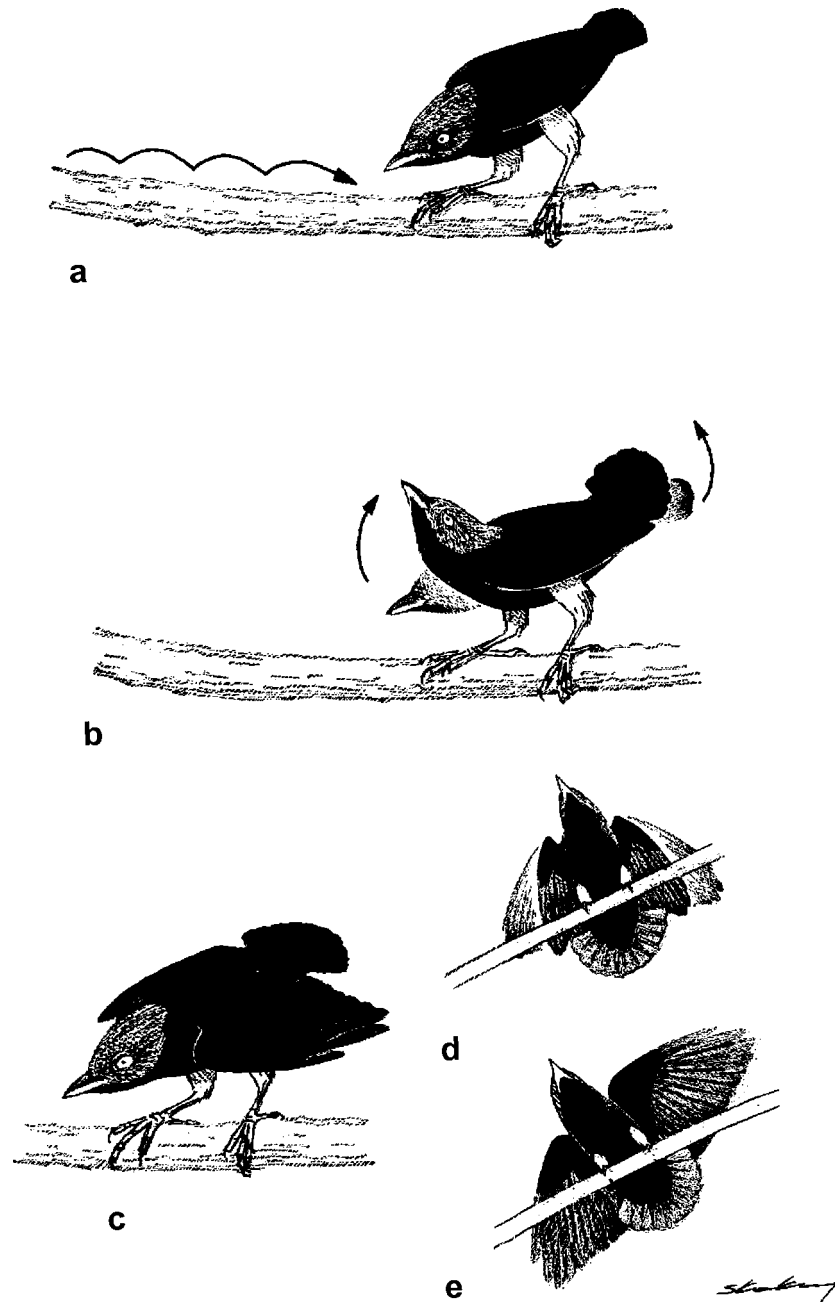


FIGURE 2. Sketches of some phases of the display dance of *Pipra chloromeros*. (a) The backward slide. (b) The U-posture at the end of the backward slide. (c), (d), and (e) The horizontal wing-spread performed at the end of the backward slide or during encounters at territory boundaries.

given by a male when a female was on his display perch. Advertisement calls may function to attract females to the arena; however, they probably also function intrasexually as territorial

calls analogous to oscine territorial songs (Lill 1976, Robbins 1983).

*Appeasement whistles.* This less frequent vocalization (4.3% of the total) is a sharp two-note

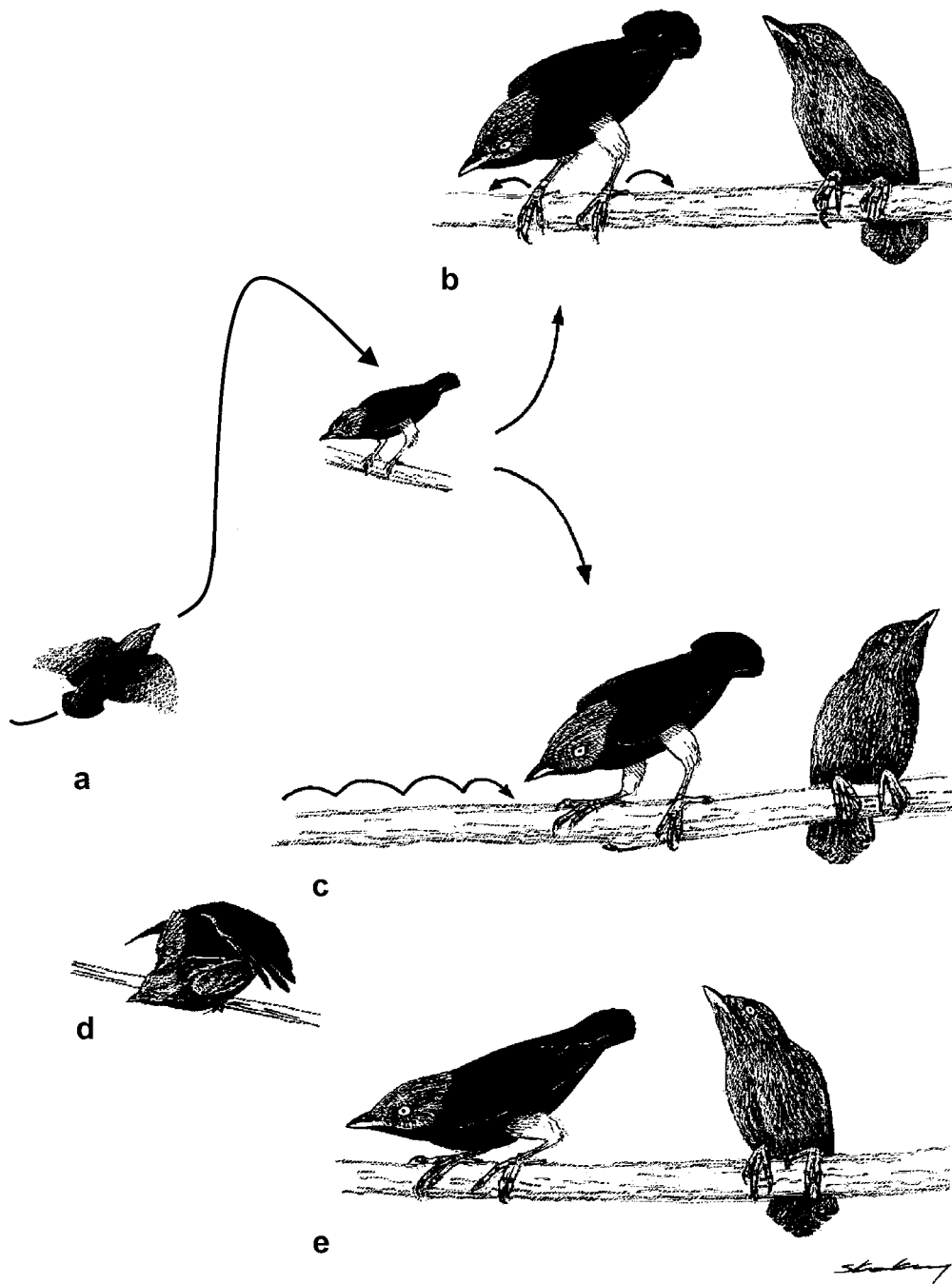


FIGURE 3. Courtship behavior of *Pipra chloromeros*. Drawings show different phases of the copulatory behavior of this species. (a) Type I flight display. (b) Squatting displays. (c) and (d) Copulations usually take place immediately after the male performs a backward slide toward the female. (e) After mating, male and female “freeze” for 15 to 30 sec.

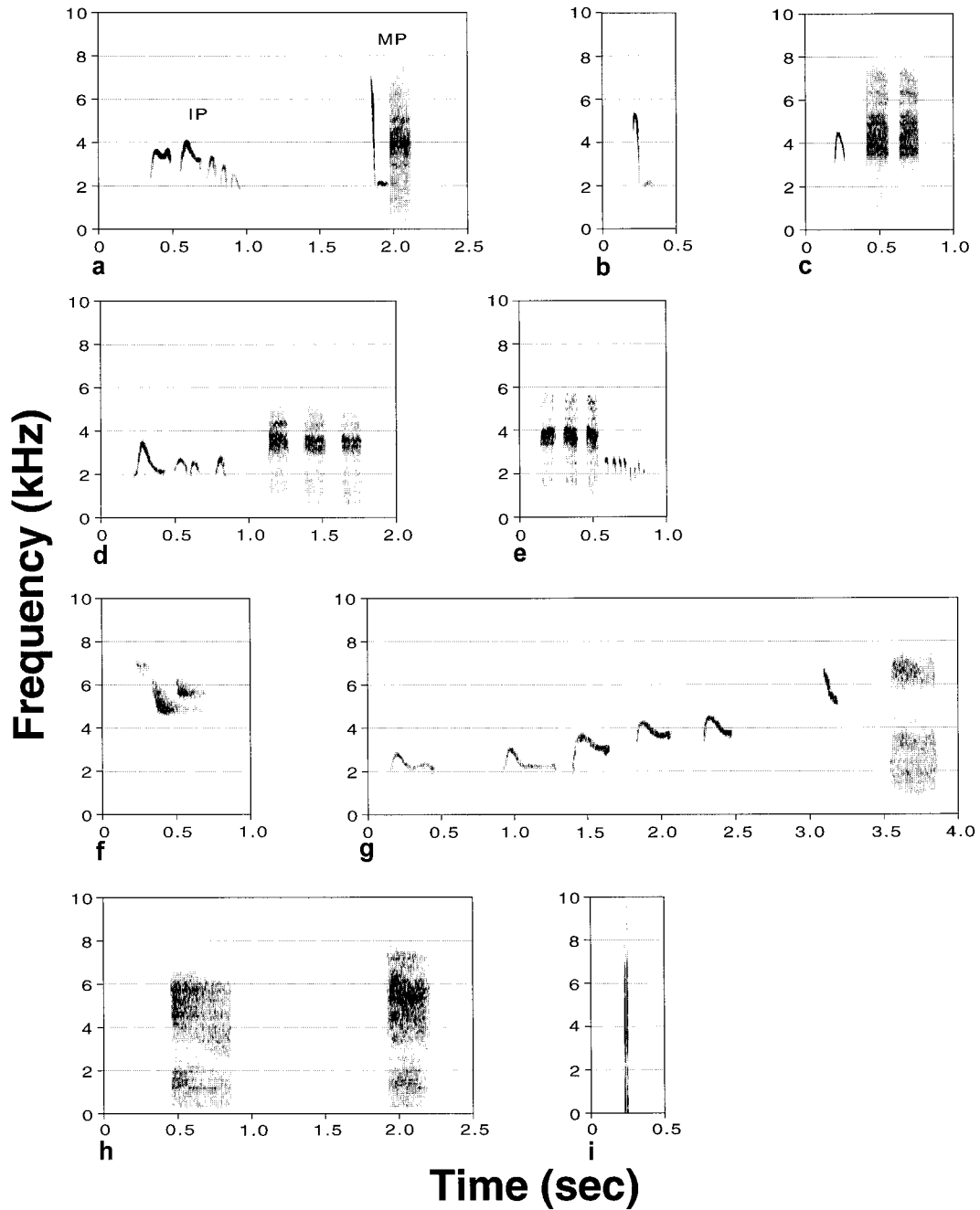


FIGURE 4. Spectrograms of vocalizations and other sounds of *Pipra chloromeros* recorded in southeastern Peru. All spectrograms were made with wide band setting. (a) Advertisement call: introductory phrase (IP) and main phrase (MP). (b) The appeasement whistle. (c) "Typical" display call. (d) and (e) Variations of the display call. (f) Type I flight display call. (g) Type II flight display call. (h) Frenzied-flutter call (= copulation call). (i) Double-wing snap.

call, *fi-u*, that lasts for about 0.1 sec (Fig. 4b). The first note is a short inverted-V whistle whose dominant frequency decreases from 5 to 2 kHz. This note is followed by a short uninflected whistle of about 2 kHz dominant frequency (Fig. 4b). Appeasement calls appeared to convey a nonaggressive state of the caller. These calls were performed by a male immediately after finishing a territorial encounter, or by a juvenile male after displaying with an adult territorial male. The call may signal that a subordinate wants to stop displaying with a dominant male. Vocalizations performed under similar circumstances have been described for *P. fasciicauda* males by Robbins (1983).

*Display calls.* The typical display call is a three-note *Fi-cuac-cuac* that lasts about 0.6 sec (Fig. 4c). The first note is a short inverted-V whistle with a dominant frequency of about 4 kHz. This whistle is followed by two buzzing notes, each with a dominant frequency of about 4 kHz. Variations of the call include a four-note call formed by a series of short whistles that are followed by three buzzing notes with slightly lower dominant frequency (Fig. 4d), or three buzzing notes followed by several whistles (Fig. 4e). These vocalizations usually were given before and during encounters among territorial males, and following outbursts of display activity at other courts within the lek, contexts similar to those described for these calls in *P. fasciicauda* (Robbins 1983). Such calls are likely used by territorial males to indicate their presence in the display area.

*Type I flight display call.* This is a short, high-pitched call, *Fu-fi-fu*, that lasts for about 0.5 sec. The call starts at a frequency of 7 kHz (first element), slides down to 5 kHz (second element), and rises to 6 kHz (third element) at the end (Fig. 4f). This vocalization was always associated with type I flight display.

*Type II flight display call.* This call is formed by a series of 6–7 short whistles that increase in frequency and intensity from 2 to 5 kHz, followed by a single buzzing note with a dominant frequency of about 7 kHz that lasts about 0.3 sec (Fig. 4g). This vocalization was always associated with type-II flight display.

*Frenzied-flutter call.* This vocalization is a two-note call, *eeee-eeee* that lasts about 1.8 sec; the elements have a dominant frequency of about 5 kHz (Fig. 4h). This call was always associated with the frenzied-flutter display and is

spectrographically similar to the call performed during copulation.

*Double-wing snap.* The double snap consists of two broad frequency pulses 0.03 sec apart with a dominant frequency of about 5 kHz (Fig. 4i). This sound is mechanically produced by the wings. Males performed this sound upon landing on the perch during the to-and-fro flight and usually during the squatting display. This mechanical sound may accent the arrival of the displaying male on the perch.

#### MALE SOCIAL STATUS AT LEKS

Observations of color-banded birds in previous manakin studies indicated that males go through a progression in social status within a lek (Lill 1976, Foster 1977, 1981). This also seems to be the case for *P. chloromeros*. I distinguished three male social categories:

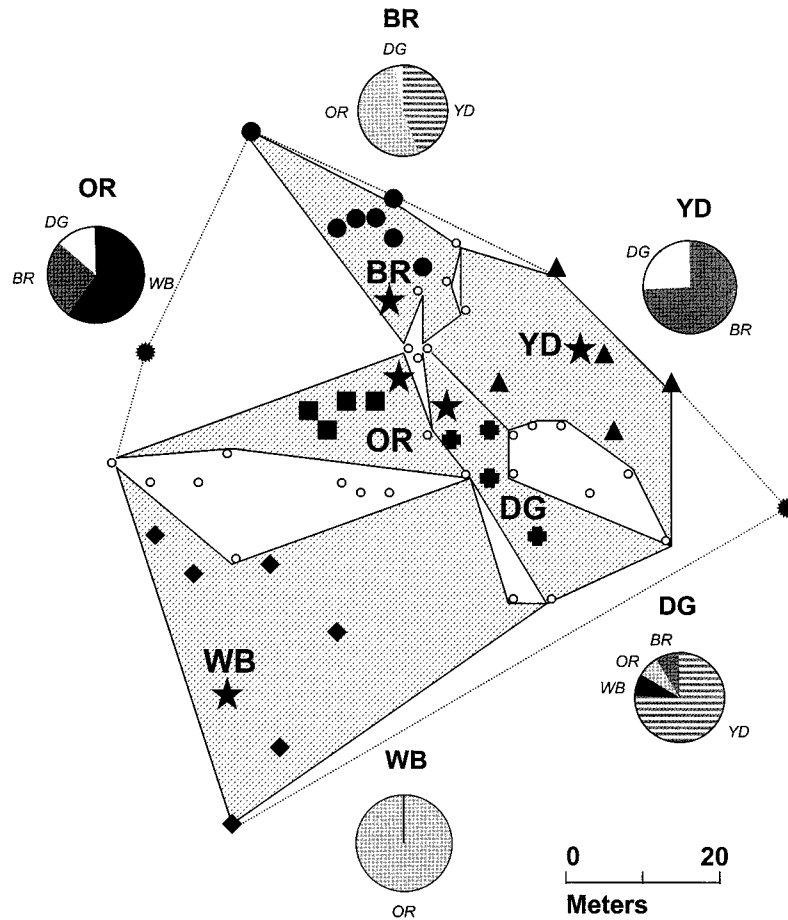
*Territorial adult males.* Males have the definitive plumage and spend most of the day and probably most of the year on the lek. These males display mainly on one perch, defending it and the court against neighbors, and they are the first to display to visiting females.

*Non-territorial adult males.* These males also have the definitive plumage and sporadically visit territorial males. These males mainly restricted their activities to peripheral areas of the lek, where they vocalized, perhaps trying to establish their own court. Non-territorial males were subordinate to territorial males, and territorial males always excluded them from their territories.

*Immature males.* These are non-territorial males in non-definitive plumages. Immature males have been observed to molt from their olive-green, female-like plumage after two reproductive periods (pers. obs.), as has been reported in other *Pipra* spp. (Lill 1976, Robbins 1985; M. Foster, pers. comm.). Young males were generally tolerated by territorial males; they were primarily observers or performed incomplete, uncoordinated displays. Some presumably older immatures performed complete displays with the territorial males and behaved more aggressively than other immature males. Occasionally, adults displayed to immature males as they did to adult females.

#### INTRASPECIFIC TERRITORIALITY

I plotted the locations of 122 boundary encounters between territorial males at one lek (Fig. 5).



**Legend** ★ = display perches; ◆ = perches of male WB; ■ = perches of male OR; ▲ = perches of male YD; ✚ = perches of male DG; ● = perches of male BR; \* = other perches used by non-territorial males; ○ = perches used in territorial encounters.

FIGURE 5. Territorial structure of lek 12 during the 1994 breeding season. Stippled areas represent the territories of resident males at this lek. Capital letters represent the identities of territorial males. Open areas are the minimal convex polygons enclosing all encounter sites (open circles) of each pair of neighboring males. The dotted and solid borders enclose the maximal estimated area of the lek. Pie diagrams show the proportions of encounters between resident males and their closest neighbors.

*Pipra chloromeros* leks consist of mutually exclusive territories (or courts). As with other lekking species, each male dominates all others on his court, and generally excludes them from it (Lill 1974, 1976, Höglund and Alatalo 1995). The three-dimensional courts appeared to be defended and maintained by ritualized agonistic encounters among territorial males; they rarely ended in fights. Encounters between pairs of territorial males took place close to the borders of

their courts on horizontal, 4.5–12 m high perches that constituted “neutral areas,” in which neither male apparently had control (Fig. 5). Neutral perches were generally located in places protected both above and on the sides by vegetation (e.g., entangled vines or clusters of dead leaves). Territorial encounters usually occurred during the morning (Fig. 6a). Before interactions took place, territorial males generally counter-sang from perches located between their courts.

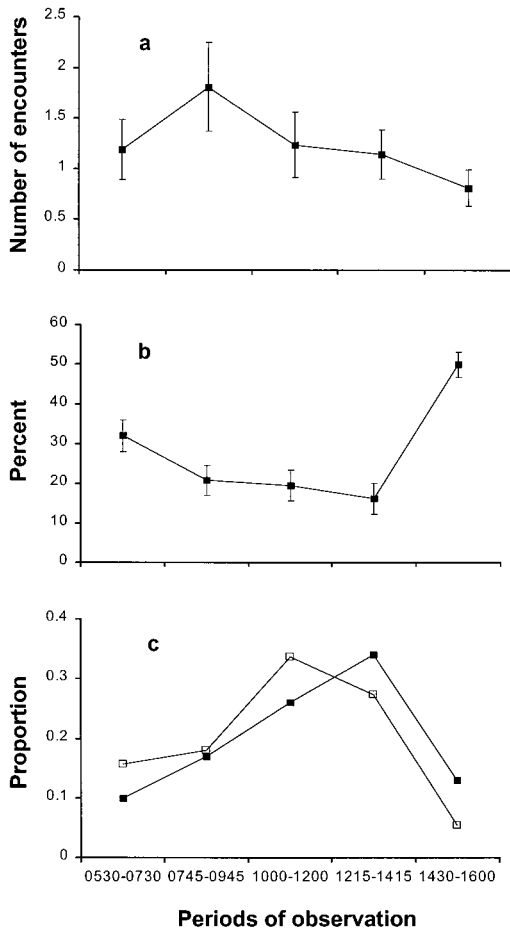


FIGURE 6. (a) Timing of daily territorial encounters at territory boundaries from two leks of *Pipra chloromeros* from Cocha Cashu. (b) Percentage of time territorial males were absent from their courts for each period of observation. (c) Calling and display activity at *Pipra chloromeros* leks. Black squares represent the proportion of time males spent vocalizing during each period of observation. White squares represent the proportion of type I flight displays performed by territorial males during each period of observation.

The display call, *Fi-cuac-cuac*, was repeated several times before and during the encounters. Neighboring males rarely engaged in fights or active displays, suggesting that they recognize each other. During encounter displays, males engaged simultaneously in wing-spreading and quivering (Fig. 7a), which they alternated with backward slides, side-to-side slides, about-faces, and wing-flicks + pivots. Wing-spreading was generally accompanied by simultaneous display calls (*Fi-cuac-cuac*, or *cuac-cuac*). Backward

sliding typically involved the approach of one male to the other, and generally ended in the other male withdrawing (Fig. 7b). During encounters, males sometimes rested close to each other for several minutes (Fig. 7c), immediately after which they displayed again. Encounters ended when one of the males abandoned the area, flying toward its court. Encounters between neighbors involved slow, coordinated displays and were similar to displays performed toward females or intruding males.

Four of seven pairs interacted often enough to analyze dominance relationships, but significant differences existed for only two interacting pairs (YD-BR and YD-DG, Fig. 5). YD never withdrew in interactions with BR (Mann-Whitney *U*-test,  $U = 18$ ,  $P < 0.05$ ) or DG (Mann-Whitney *U*-test,  $U = 12$ ,  $P < 0.05$ ). In contrast, WB frequently approached OR but was not obviously dominant based on the low number of OR withdrawals (Mann-Whitney *U*-test,  $U = 44$ ,  $P > 0.05$ ). These findings suggest that some degree of dominance may exist. Further, dominance relationships may change over time (Robbins 1985). I rarely saw widely separated males interact at lek 12 (i.e., males WB and YD in Fig. 5). At lek 10, where territorial males rarely interacted, intermale distance averaged about four times greater than at lek 12.

On three occasions, I observed more complex, coordinated flight displays at the main perches of three males. The interactions involved a territorial male and an adult or immature male visitor, but never two territorial males. The two displaying birds alternated a series of stereotyped displays that included (in order of occurrence): upright postures, wing-flicks + pivots, display calls, squats, type I flight displays and associated calls, backward slides, and the U-posture (Fig. 8). The displays started with the two males holding the upright posture for a few seconds, immediately after which "male 1" performed a series of wing-flicks + pivots before flying to another perch ca. 7 m away from the display perch. He then uttered a type I display call, and gave a type I flight display and flew back to the original perch (Fig. 8a). At the same time, "male 2," which was giving the display call, performed an about-face and several squatting displays, moving away from the center of the display perch (Fig. 8b). When male 1 landed on the perch, both males performed simultaneous backward slides toward each other (Fig. 8c, d). This

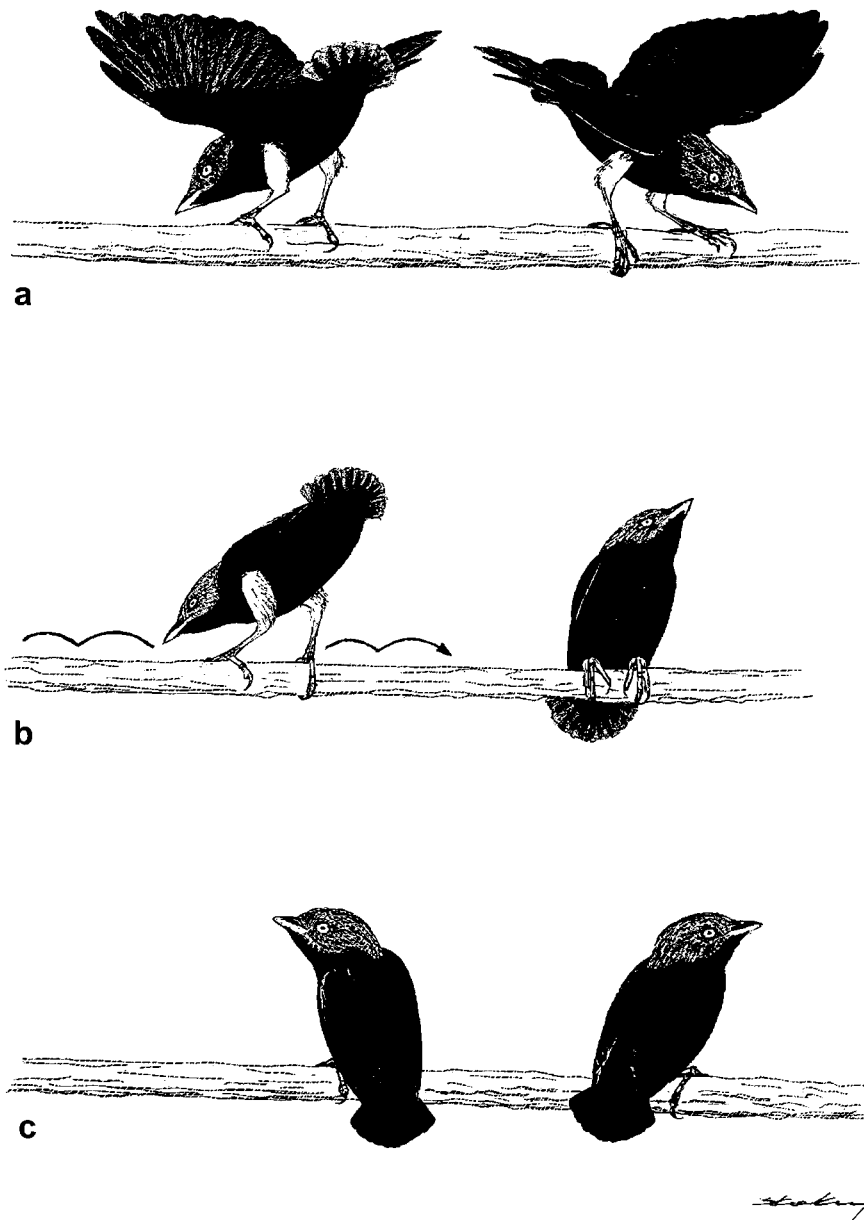


FIGURE 7. Coordinated ritual display at territory boundaries. (a) Neighboring males display together and perform a display call. (b) One male approaches the other using a backward slide, which occasionally causes the other male to withdraw. (c) During the encounters, resident males rest close to each other for some minutes until they start to display again.

was followed by the U-posture held until both males depressed their tails, which appeared to touch each other (Fig. 8e). They gave this display (backward slide + U-posture) twice. Then, one of the birds uttered a display call to which the other male responded. Suddenly, male 2 flew

away from the display perch and repeated the same coordinated flight display. The two males alternated, performing a total of 26 (13 each) of these coordinated flight displays for almost 5 min. Sometimes, the bird that remained on the display perch performed a series of to-and-fro

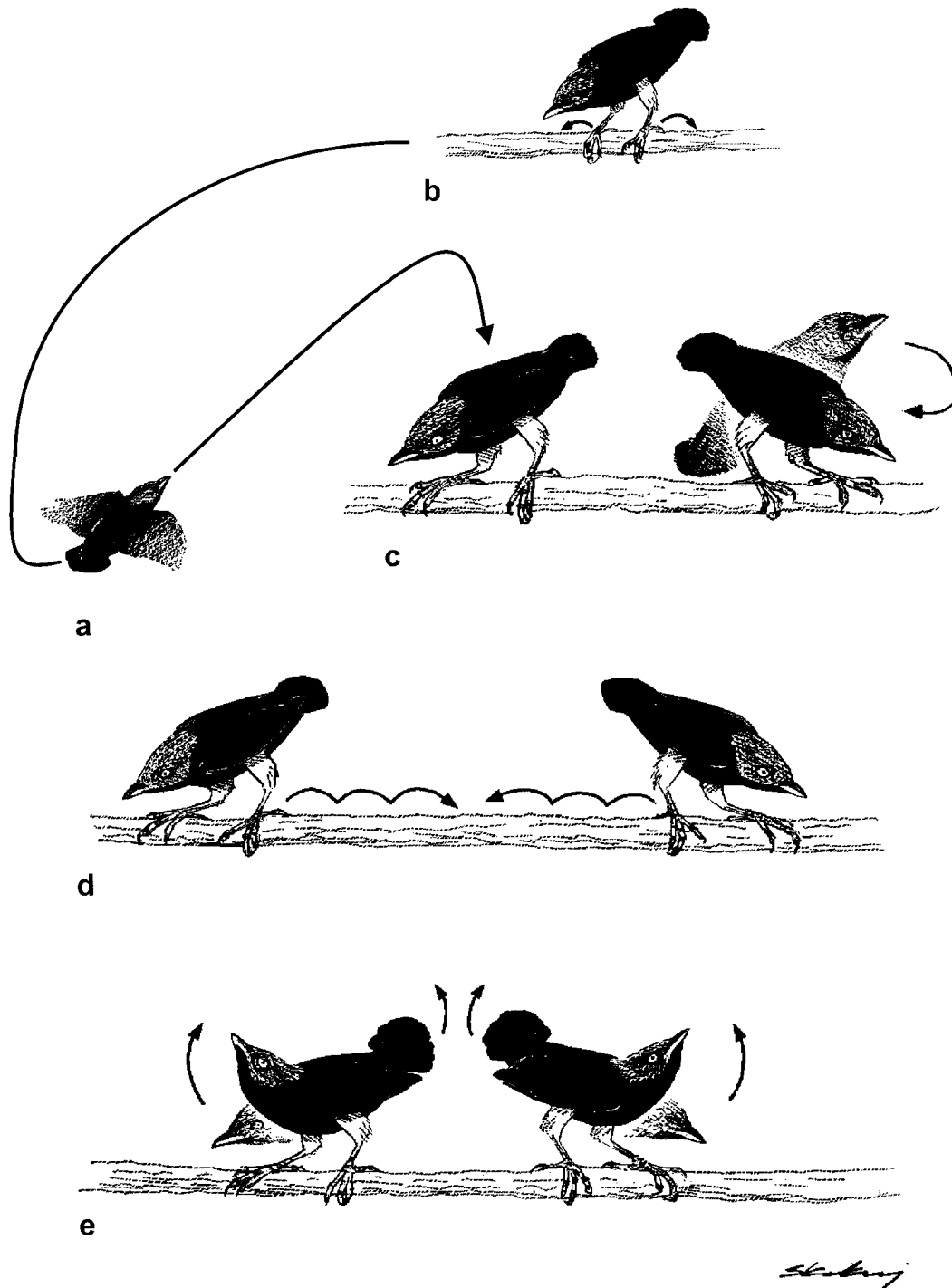


FIGURE 8. Coordinated flight displays at one male's territory. (a) After flying away from the main perch, one of the males returned with a type I flight display, uttering a type I flight display call upon landing. (b) At the same time, the second male, which was giving the display call, performed several squatting displays. (c) and (d) When the former bird landed on the perch, both males performed simultaneous backward slides toward each other. This was followed by the (e) U-posture held until both males depressed their tails, which appeared to touch each other. Then, both birds uttered display calls, until the latter bird flew away and re-initiated the displays.

flights, followed by squatting displays, before the other male landed on the main perch. After resting for two minutes while maintaining the upright posture, the males reinitiated the display, but this time they performed only six (three each) coordinated flight displays. The displays ended when male 2 abandoned the perch. Interactions involving coordinated flight displays have been observed to occur under similar circumstances in *P. fasciicauda* (Robbins 1983) and *P. mentalis* (pers. obs.).

#### INTERSPECIFIC TERRITORIALITY

*Pipra chloromeros* males showed a certain degree of interspecific territoriality around their display areas. I observed territorial males chasing males of two other manakin species, *P. coronata* and *P. fasciicauda*, when they approached their display areas. Other birds, such as the White-winged Shrike-Tanager (*Lanio versicolor*), Orange-bellied Euphonia (*Euphonia xanthogaster*), and Dusky-throated Antshrike (*Thamnomanes ardesiacus*) were also excluded. Territorial males usually displayed actively on their display perches when a mixed-species flock moved through their courts, but males did not chase flock species. Occasional presence of females or young males of *P. chloromeros* in these flocks also caused males to display.

#### SEXUAL BEHAVIOR

*Pipra chloromeros* breeds mainly from early August to the end of November. Female visits were recorded mostly during midday (10:00–14:30). Most visits ( $n = 9$ ) were by a single female, but once I recorded two females visiting a single male at the same time. Lill (1976) recorded some *P. erythrocephala* females visiting males in pairs, and Foster (1977) also reported pairs of females visiting a single *Chiroxiphia linearis* male.

*Territory attendance.* Males were present on their territories from 58% to 85% of the observation time (mean =  $73.3 \pm 3.3\%$ ). The proportion of time that males were absent from their territories varied significantly among observation periods (ANOVA:  $F_{4,92} = 5.2$ ,  $P < 0.001$ ), being greater during late afternoon (14:30–16:00; mean = 50.2% of male absenteeism) than at any other time (Fig. 6b). During hours when most females were recorded visiting the lek (10:00–14:30), males were absent from their display areas only 20% of the time. During those

hours, feeding bouts were short and directed mainly to fruiting trees or shrubs within the male's territory. In the early morning (06:00–07:00) and late afternoon (after 15:00), males spent significantly more time (mean = 4.8 min per feeding bout) feeding in fruiting trees than they did during the middle of the day (mean = 1.3 min per feeding bout;  $U = 67.5$ ,  $P < 0.01$ ).

*Courtship behavior.* Calling activity at the leks (based on number of advertisement calls) was most intense from 12:00 to 14:30 (Fig. 6c; ANOVA:  $F_{4,104} = 6.5$ ,  $P < 0.001$ ). Display activity (based on number of type I flight displays) also varied significantly during the day (Kruskal-Wallis,  $\chi^2_4 = 12.0$ ,  $P < 0.05$ ); activity was concentrated between 10:00 and 14:30 (Fig. 6c).

As expected, hours when female visitation was highest (10:00–14:30) coincided with outbursts of display activity within the leks. Unfortunately, because the cryptically colored females are difficult to detect unless they move, it was not always possible to tell if the arrival of a female stimulated males to display or the outbursts of male display attracted the females. The lack of significant differences in display activity (based on frequency of flight displays) between the successful males (those which obtained all the observed copulations) and other territorial males at one lek (Kruskal-Wallis,  $\chi^2_4 = 3.2$ ,  $P > 0.05$ ) suggests that the outburst of male display activity may be a response to a female visiting the lek. The small number of observed copulations makes it difficult to generalize, however. Apparently, males at a lek have a mutually stimulating effect, so that when one starts to display a general increase in activity results (Snow 1962, Lill 1976).

*Copulatory behavior.* The five observed copulations took place between 13:00 and 14:30. Copulations followed displays on the main perch including all or several of the following display elements: type I flight displays, backward slides, about-faces, to-and-fro flights, squats, wing-flicks, pivots, and the upright posture (Fig. 3a–c). In contrast to Lill's (1976) observations of *P. erythrocephala* females (which might have been immature males) participating with males in the courtship displays, I only saw *P. chloromeros* females in an upright posture (Fig. 3b, c, e). Females sometimes delivered very light pecks to the male's head feathers as he approached her. This behavior is also known for *P. erythrocephala* (Lill 1976) and the Guianan Cock-of-the-

TABLE 3. Number of visits by females and immatures, copulations, advertisement calls, flight displays, and agonistic encounters at two *Pipra chloromeros* leks of different size. \*  $P \leq 0.05$ , Mann-Whitney  $U$ -test.

Sexual attraction and display level measures	Total		Average per male	
	Lek 12 <sup>a</sup>	Lek 10 <sup>a</sup>	Lek 12	Lek 10
Visits by females	7*	0	1.4	0
Visits by immatures	9	6	1.8	3.0
Observed copulations	3	0	0.6	0
Advertisement calls	1473*	608	294.6	304.0
Flight displays	103*	25	20.6	12.5
Agonistic encounters	122*	8	24.4*	4.0

<sup>a</sup> Lek 12 = 5 males; Lek 10 = 2 males.

Rock (*Rupicola rupicola*, Snow 1971). Copulations were immediately preceded by (1) Type I flight displays in which the male landed beside the female on the display perch and then jumped onto her back ( $n = 2$ ); (2) backward slides, following which the male jumped onto and covered the female ( $n = 2$ ); or (3) a squatting display ( $n = 1$ ).

Copulations lasted 2 to 4 sec, during which the male beat his wings and emitted two buzzing notes (Fig. 3d). Immediately after mating, the pair froze for about 15 to 30 sec (one pair froze for nearly 100 sec), with the male maintaining a horizontal posture (parallel to the perch) and the female maintaining the upright posture (Fig. 3e). During this time, females were observed to contract the cloacal opening. Freezing and cloacal closure may help the female to retain sperm. The male then began to perform a series of squatting, backward slide, wing-flick, pivot, flight display, and to-and-fro flight displays, perhaps trying to copulate again with the same female. One male copulated twice in 15 min, but I could not determine if the same female was involved. After a female departed, males usually continued displaying vigorously for a few minutes, and then either resumed advertising or abandoned the court.

Measures of sexual attraction, calling activity, and display activity differed somewhat between two *P. chloromeros* leks, one with two males and the other with five (Table 3). Female visitation and copulations were seen only at the larger lek, where two males received all the observed visits ( $n = 7$ ) during the focal samples. In contrast, total number of visits by immatures did not differ between leks. Overall calling and display activity were greater at the larger lek but, on average, individual males at this lek did not call or display more than did males at the small-

er lek (Table 3). Encounters among territorial males were more frequent at the larger lek, and individual males from the larger lek were involved in significantly more territorial encounters than those from the smaller lek.

## DISCUSSION

### LEK ORGANIZATION

Based on numbers of males (two to five) and the diameters of their territories ( $>20$  m), leks of *P. chloromeros* are more similar to those of *P. cornuta* (Snow 1977) and *P. rubrocapilla* (pers. obs.) than to those of *P. mentalis* (Skutch 1949, 1969; pers. obs.) and *P. erythrocephala* (Snow 1962, Lill 1976). Using Prum's classification of lek spatial organization (1994), the leks of the former three species fall into the category of dispersed leks, whereas *Pipra mentalis* and *P. erythrocephala* have concentrated leks (Table 1 in Prum 1994).

### INTRASPECIFIC TERRITORIALITY

In general, the nature of interactions among territorial males of *P. chloromeros* was similar to those among male *P. erythrocephala* (Lill 1976). However, the behaviors of these two species contrast with descriptions of male-male interactions in other manakins such as *Manacus manacus* (Lill 1974) or *P. coronata* (M. Foster, pers. comm., pers. obs.) in which the outcomes of male boundary encounters were more easily determined.

The nature of these encounters suggests that court boundaries constitute "neutral zones," instead of finite lines, in which no male completely dominates neighboring males (Lill 1974, 1976). Such coordinated displays between males occur in other manakins of the same clade (e.g., in *P. erythrocephala*, Lill 1976, Snow 1962; in *P. rubrocapilla*, Sick 1959a, 1967; in *P. men-*

*talis*, Skutch 1949, 1969). Encounters at territory boundaries have been suggested to function in establishing and maintaining dominance relationships among males (Foster 1981, Bradbury and Davies 1987). Observations of female-plumaged birds interacting as adults on perches far from any known lek (pers. obs.) indicate that these interactions start early in the male's life.

#### EFFECT OF LEK SIZE ON FEMALE ATTRACTION AND OVERALL MALE BEHAVIOR

Variation in lek size within a study population has been recorded for several lekking species (Höglund and Alatalo 1995). This variation may be influenced by various factors, including: (1) the number of females using a patch of habitat near the lek (Bradbury and Gibson 1983); (2) the quality of the alpha male(s), that may cause other, less successful males to cluster around those "hotshots" (Beehler and Foster 1988); and (3) the structure of the habitat in which the leks are located (Olson and McDowell 1983). Within a population, smaller leks may be short-lived, eventually driven to extinction as a result of female preferences for larger clusters of males (Bradbury 1981, Beehler and Foster 1988). Display levels in large leks are expected to be more intense than those in small leks due to social facilitation (closer male territories; Lack 1939, 1946). The high level of display and calling activity at large leks probably exert disproportionately attractive and stimulative effects on females (Alatalo et al. 1991). If so, then males displaying in larger groups should have a higher mean reproductive success than males in smaller groups.

The lekking behavior of *P. chloromeros* reported here leads to some interesting observations, even given sample size limitations: (1) It is unlikely that differences in female abundance explain the observed differences in lek size, because the leks were only approximately 670 m apart. The observed distance between leks falls within the female home-range size estimated for other *Pipra* species (Thery 1992), and manakin females can include more than one lek in their home ranges (Thery 1992; M. Foster, pers. comm.). Thus, it is possible that both leks could have been visited by the same females. (2) Contrary to expectation, (following Bradbury 1981 and Beehler and Foster 1988), both leks maintained the same number of males during 7 years.

(3) Overall activity was greater at the larger lek, but the numbers of vocalizations and displays that each male performed did not differ significantly. Thus, males at the smaller lek did not necessarily call or display more to compensate for their lower numbers, and so increase their "radius of attractiveness" (Bradbury 1981). (4) Males at the larger lek were surrounded by more neighbors and so might be expected to expend more time in territorial encounters than males at the smaller lek (Lill 1976, Beehler and Foster 1988). This was confirmed by the higher overall number of territorial encounters recorded at the larger lek ( $n = 122$ ) compared with that recorded at the smaller one ( $n = 8$ ). Individually, males from the larger lek were involved in more total interactions (mean =  $24.4 \pm 5.8$ ) than those from the smaller one (mean =  $4.0 \pm 0.6$ ). Finally, (5) the fact that females visited only two of five males at the larger lek suggests that non-alpha males would not gain much from clustering, at least in the short term. Lill's (1976) studies of leks of *P. erythrocephala* showed similar results; males at smaller leks were not at a selective disadvantage, and on average had sexual success similar to those of males at larger leks, supporting the hypothesis that lek size is determined by the effect of particularly successful males (Beehler and Foster 1988, Alatalo et al. 1991). However, other factors, such as vegetation structure at the lek could also constrain the number of males at one site. More studies on habitat characteristics of lek sites, as well as long-term studies of mating success and tenure of alpha males, are required to fully answer questions related to lek formation and maintenance.

#### EVOLUTIONARY IMPLICATIONS OF *PIPRA CHLOROMEROS* DISPLAYS

The genus *Pipra* is divided into two clades: the *P. erythrocephala* clade (*cornuta*, *mentalis*, *erythrocephala*, *chloromeros*, and *rubrocapilla*) and the *P. aureola* clade (*aureola*, *fasciicauda*, and *filicauda*) (Prum 1992). Vocalizations and displays are remarkably similar between *P. chloromeros* and other members of the *P. erythrocephala* clade (Table 4). In his study on the evolution of manakin displays, Prum (1990) recognized 11 different displays for the *P. erythrocephala* clade. Four of those displays (horizontal posture, frenzied-flutter, to-and-fro flight, and type I flight display) are present primarily in the

TABLE 4. Comparison of displays within the *Pipra erythrocephala* clade. Signs +, -, or ? indicate the presence, absence, or uncertainty of a behavior in the species' repertoire.

Display	<i>P. cornuta</i> <sup>a</sup>	<i>P. mentalis</i> <sup>b</sup>	<i>P. erythrocephala</i> <sup>c</sup>	<i>P. chloromeros</i> <sup>d</sup>	<i>P. rubrocapilla</i> <sup>e</sup>
<b>Vocal</b>					
Advertisement call, display call, type II flight display call	+	+	+	+	+
Appasement whistle	?	+	+	+	?
Type I flight display call	?	-	-	+	?
Frenzied-flutter call	?	+	+	+	+
<b>Mechanical</b>					
Mechanical wing noise with to-and-fro flight					
In flight	+	+	-	-	-
After landing	+	+	-	+	-
Mechanical wing-snapping associated with wing-flicking (wing-snapping twist display)					
Mechanical noise at the end of squat	?	+	-	-	-
Mechanical noise associated with type II flight display	?	+	-	+	?
Wing noise at end of backward slide	+	?	-	+	-
About face	?	+	+	+	+
Upright posture, to-and-fro flight, backward slide	+	+	+	+	+
Wing position during backward slide	Slightly raised	Against body; may hold wings above back	Against body; may momentarily spread wings horizontally	Against body	Slightly raised
Tail position during backward slide					
Tail-shivering during backward slide	Depressed	Elevated	Elevated	Elevated	Depressed
Horizontal wing-quivering and tail-fanning at end of backward slide	-	+	-	-	-
Momentary wing-spreading and tail-fanning at end of backward slide	?	-	-	+	+
Horizontal; tail position unknown	Horizontal; tail position unknown	Vertical; tail raised	Vertical; tail depressed	Horizontal; tail depressed	Horizontal; tail depressed
U-posture at end of backward slide					
Backward slide with forward rebound	-	-	-	+	-
Side-to-side slide	+	+	+	+	-
Wing-flicking	?	+	+	+	?
Nominate vocal snapping sound associated with wing-flicking	?	-	-	-	+

TABLE 4. Continued.

Display	<i>P. cornuta</i> <sup>a</sup>	<i>P. mentalis</i> <sup>b</sup>	<i>P. erythrocephala</i> <sup>c</sup>	<i>P. chloromeros</i> <sup>d</sup>	<i>P. rubrocapilla</i> <sup>e</sup>
Squatting	?	+	+	+	?
Flight displays					
Type I (Swoop-in flight)	+	+	+	+	+
Type II (Catapult flight)	?	+	+	+	+
Frenzied-flutter	+	+	+	+	+
Horizontal freeze	?	+	+	+	?
Wing-raising display	-	-	-	-	+
Coordinated display between males					
Coordinated ritual display	?	+	+	+	+
Coordinated flight display	?	+	?	+	?

<sup>a</sup> Snow 1977, R. O. Prum unpubl. data.

<sup>b</sup> Chapman 1929, Crandall 1945, Skutch 1949, 1969.

<sup>c</sup> Snow 1956, 1962, Lill 1970, 1976.

<sup>d</sup> Niethammer 1956, Tello 1996, L. Kinkel in Prum 1990.

<sup>e</sup> Sick 1959a, 1959b, 1967, 1993.

genus *Pipra*; five (upright posture, about-face, backward slide, double-wing snaps with to-and-fro-flight, and the buzzing noise with type II flight) are found only in the *P. erythrocephala* clade and are probably derived; and two constitute displays that prior to this study were found only in the repertoire of *P. cornuta* (side-to-side slide and backward slide with forward rebound; Table 4). Because, at the time of Prum's work, the lekking behavior of *P. chloromeros* was poorly known, I decided to compare the behaviors of the species in this clade in more detail based on reanalysis of the literature on displays (Table 4). Although observations for *P. cornuta* are still incomplete (Snow 1977), some interesting trends are apparent among these five species.

Type I flight display is derived in *Pipra* (Prum 1990), and usually includes a high-pitched short call given by the male upon landing (present in *P. fasciicauda*), which may have evolved simultaneously with the flight display (assuming that the call is present in *P. cornuta*). The call is absent from *P. mentalis* and *P. erythrocephala*, and is unknown in *P. rubrocapilla*. Type II flight display (catapult-like flight) probably constitutes a variation of type I flight display that is derived in the *P. erythrocephala* clade. As in type I, the bird vocalizes when it lands. The vocalization consists of a single or multiple note call (Fig. 4g) that always ends with a buzzing note given as the bird arrives at the display perch. In general, the structures of associated calls as well as the context in which flight displays are performed differ among species within the *P. erythrocephala* clade. Type I flight display is used mainly during courtship by *P. chloromeros*, which performs type II mostly during interactions with non-territorial males. In contrast, *P. mentalis* and *P. erythrocephala* use type II displays mainly during female courtship (Lill 1976, pers. obs). Thus, between *P. mentalis* and *P. erythrocephala*, the primary function of type II flight display has changed.

Structural modifications of secondary feathers have allowed the production of mechanical sounds in manakins (Sick 1967, Prum 1998). In *Pipra* spp., several displays have evolved to incorporate mechanical noises, perhaps in order to increase the conspicuousness of the display and to attract the attention of the visiting bird toward the main display area. Mechanical noises have been recorded in three (*P. cornuta*, *P. mentalis*, and *P. chloromeros*) of the five members of the

*P. erythrocephala* clade. As expected, the two species from which mechanical noises are absent (*P. rubrocapilla* and *P. erythrocephala*) also lack the associated modifications of the secondary wing feathers (Prum 1998). Displays in which mechanical noises are found include to-and-fro flight, squatting display, type II flight display, and the stereotyped wing-snapping twist display (only described for *P. mentalis*).

Mechanical noises associated with the to-and-fro flight are controlled wing snaps performed while flying (*P. cornuta*, *P. mentalis*), or immediately after landing (*P. cornuta*, *P. mentalis*, *P. chloromeros*). Mechanical wing noises associated with the squatting display are present in *P. chloromeros* and *P. mentalis* (pers. obs.), and are unknown in *P. cornuta*. Sometimes, birds make a whirring mechanical noise upon landing after a type II flight display (the mechanical-noise flight, Prum 1990). These noises are made by *P. mentalis* and *P. chloromeros* but are unknown in *P. cornuta*.

One of the more unusual behaviors described in the *P. erythrocephala* clade is the wing-snapping twist display of *P. mentalis* (Skutch 1949, 1969). This display may have evolved from the about-face movement (a trait found primarily in *Pipra*) and wing-flicking (a common display in Pipridae and other Tyrannoidea). Males of *P. rubrocapilla* also include snapping sounds in their display repertoires (Library of Natural Sounds 32030), but because the secondary feathers are not modified, these sounds presumably have a vocal instead of a mechanical origin (Sick 1967). These sounds are associated with about-faces and wing-flicks as they are in *P. mentalis* (Sick 1967).

The upright posture is a derived display in the *P. erythrocephala* clade (Prum 1990) that is performed by all the members of the group without apparent modifications. The orientation of a male's posterior toward a visitor is also widespread in *Pipra* (Sick 1967, Robbins 1983, Prum 1990). This behavior can be found in the tail-up freeze of *P. fasciicauda* (Robbins 1983) and the backward slide of the *P. erythrocephala* clade (Prum 1990).

The backward slide and side-to-side slide are elaborate displays that apparently evolved from the horizontal posture (primitively present in the genus *Pipra*, Prum 1990). Prum (1990) suggested that the backward slide and side-to-side slide displays are derived in the *P. erythrocephala*

clade. However, similar displays have been recorded for the *P. aureola* clade (Snow 1963b, Schwartz and Snow 1978, Robbins 1983), which may place the evolution of these displays with an ancestor of these two clades. Snow (1963b) described the side-to-side and backward-and-forward displays of *P. aureola* as movements in which the bird literally slides on the perch. Although Schwartz and Snow (1978) described the side-to-side display of *P. filicauda* as a movement in which the bird jumps very rapidly to one side on the perch, they also noted the similarity of backward jumps of this species to the sliding displays observed in other *Pipra*. In the same way, Robbins (1983) described the side-to-side display of *P. fasciicauda* as jumps or hops to one side of the perch, but he also pointed out that from the tail-up freeze position (a modification of the horizontal position), the male may back toward the visiting bird while performing this display. This strongly suggests that backward slides and side-to-side slides arose in the ancestor of *Pipra*, and were then modified to include jumps (side-to-side), or to largely disappear (backward slide only) in the repertoires of *P. filicauda* and *P. fasciicauda*. This also suggests that *P. filicauda* and *P. fasciicauda* might be sister species, which would explain the presence of jumps in the side-to-side display of these two species.

The side-to-side slide is apparently absent from *P. erythrocephala*, and is unknown in *P. rubrocapilla*. Most of the members of the *P. erythrocephala* clade (Prum 1990) usually end the backward slide with a horizontal wing-spreading and fanning of the lowered tail. *Pipra mentalis* and *P. erythrocephala*, in contrast, raise their wings vertically above the back and simultaneously lower and fan the tail. In this group, the backward slide serves as the base for addition of terminal movements and postures, such as the tail-shivering of *P. mentalis* (Skutch 1949, 1969), U-posture of *P. chloromeros*, and forward rebound of *P. cornuta* (Snow 1977). Other variations of the backward slide include: (1) tail slightly depressed and wings slightly raised during sliding (*P. cornuta* and *P. rubrocapilla*); (2) wings held above the back during the slide (*P. mentalis*; Skutch 1949, 1969); and (3) rapid opening and closing of wings halfway down the slide (*P. erythrocephala*, Table 4).

Within the *P. erythrocephala* clade, differences in visual stimulation (display movement and

thigh coloration) exhibited to females during the backward slide may constitute important isolating mechanisms. Displays in which males orient their posteriors toward a female or other visitor have been suggested as one of the factors promoting the evolution of striking plumage patterns in some manakins (Robbins 1983). During the backward slide, males of the *P. erythrocephala* clade straighten their legs to show their feathered thighs (bright yellow, white-red, or red). Backward slides and colored thighs are both derived characters in this group. Thus, it seems that both characters arose at the same time without any apparent influence on one another. Another example of simultaneous origin of behavioral and plumage characters is found in the wing-raising display of *P. rubrocapilla*, and the wing-snapping twist display of *P. mentalis*. These postures would serve as a visual stimulus to the female during courtship, by showing the conspicuous white and yellow underwing spots. These postures have not been recorded in the other three species, which lack underwing color spots.

Advertisement calls in the *P. erythrocephala* clade share features that make them different from calls of the members of the *P. aureola* clade. In the *P. erythrocephala* clade, advertisement calls are composed of several elements (e.g., different types of whistles, buzzing notes, and trills), whereas in the *P. aureola* clade, advertisement calls are composed of a single downwardly inflected whistle (Snow 1963b, Schwartz and Snow 1978, Robbins 1983). In the *P. erythrocephala* clade, an introductory and a main phrase are usually distinguished in the advertisement call (Skutch 1949, Snow 1962, Sick 1967, Lill 1976). The frenzied-flutter call is found only in the *P. erythrocephala* clade; in the *P. aureola* clade the display is silent (Schwartz and Snow 1978, Robbins 1983). Other vocalizations, such as display calls and appeasement whistles, are also found in some members of the *P. aureola* clade (Robbins 1983).

Male-coordinated displays (both the ritual display and the active flight display) in the *P. erythrocephala* clade seem to be more important for dominance relationships than for mate attraction. This is supported by the observation that both ritualized and actively coordinated displays are performed by males in the absence of females. The lack of more aggressive displays among territorial males in the *P. erythrocephala* clade

probably is a consequence of greater intermale distances (Foster 1983). In *P. chloromeros*, I never observed a territorial male visit the main display perch of another territorial male. Ritual displays may reflect previous aggressive interactions among neighboring males.

Eighteen of the 34 display elements present in the *P. erythrocephala* clade have also been recorded in the *P. aureola* clade. The remaining 16 display elements are present only in the *P. erythrocephala* clade, and seven of those elements constitute behavioral autapomorphies of a particular species. Not surprisingly, all display novelties were associated with displays particularly important during female courtship (e.g., the backward slide, Table 4). The great diversity of displays observed in the *P. erythrocephala* clade could have arisen under intense sexual selection (particularly intense in polygynous systems) acting on displays important for mate selection (Lande 1981, West-Eberhard 1983, Prum 1997). At some point following geographic isolation, behavioral differences among closely related forms would probably be enough to prevent mating and cause reproductive isolation.

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