DISPLAY BEHAVIOR AND NATURAL HISTORY OF THE YELLOW-CROWNED MANAKIN (*HETEROCERCUS FLAVIVERTEX*: PIPRIDAE)[1]

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Abstract. The behavior and natural history of the Yellow-crowned Manakin (*Heterocercus flavivertex*, Pipridae) were observed on the Rio Ventuari in northern Territorio Federal Amazonas, Venezuela. Male *flavivertex* have a solitary lek breeding system, a display repertoire including five distinct vocalizations, several display elements, and a probable mechanical display sound. The tail-shiver display, in which the cocked tail is prominently featured, has not been observed in other *Heterocercus* species, but this display element may be an explanation for the evolution of the unique tail shape in the genus. Other *flavivertex* display elements, such as the above-the-canopy display flight, are behavioral homologs shared with other *Heterocercus* species. Female *H. flavivertex* construct hanging cup nests that are similar in architecture, composition, and placement to other manakin species. The diet of *H. flavivertex* is apparently composed of a greater quantity of insects than other manakin species. The evolution of display, morphology, diet, and social behavior in *Heterocercus* is discussed.

Key words: lek; courtship; display; song; manakins.

INTRODUCTION

The Neotropical manakins are well known for their striking sexually dimorphic plumage, elaborate courtship displays and lek breeding systems (Snow 1963b, Sick 1967, Prum 1990a, 1994). Comparative studies of the manakins demonstrate that lek breeding is primitive to the family, and that many aspects of manakin display and reproductive behavior vary phylogenetically among closely related genera and species of manakins (Prum 1990a, 1990b, 1992, 1994). Although the behavior of many manakin species has been studied in detail, there are no published accounts of the behavior and natural history of almost half the species in the family (Prum 1990a, 1994). Additional work on these poorly known species is essential to advancing our understanding of the evolution of behavior of the family.

The genus *Heterocercus* includes three species that are among the most poorly known manakins. The Yellow-crowned (*H. flavivertex*), Flame-crowned (*H. linteatus*), and Orange-crowned (*H. aurantiivertex*) Manakins are distributed allopatrically around the Amazonian basin (Fig. 1; Snow 1979, Haffer 1986, Ridgely and Tudor 1994). All three species live in seasonally flooded varzea forests, blackwater riparian or sandy soil woodlands (Hilty and Brown 1986, Sick 1993, Ridgely and Tudor 1994, R. O. Prum, pers. observ.). The genus is characterized by dark green upperparts, chestnut underparts, a sexually dimorphic white throat patch with long side plumes, carotenoid-colored crown patch, and an unusually graduated tail with the outer rectrices shortest (Fig. 2). The behavior of *Heterocercus linteatus* is known only from a single anecdotal observation by Sick (1959, 1967, 1993). Sick described the advertisement call of *linteatus* as *piteew*, and stated that *linteatus* displays by spreading the throat patch feathers to the sides like a "broad beard" (Sick 1993). There are no other published observations of the vocalizations, displays, breeding system, nest, or diet of the genus. We conducted field work on *Heterocercus flaviv-*
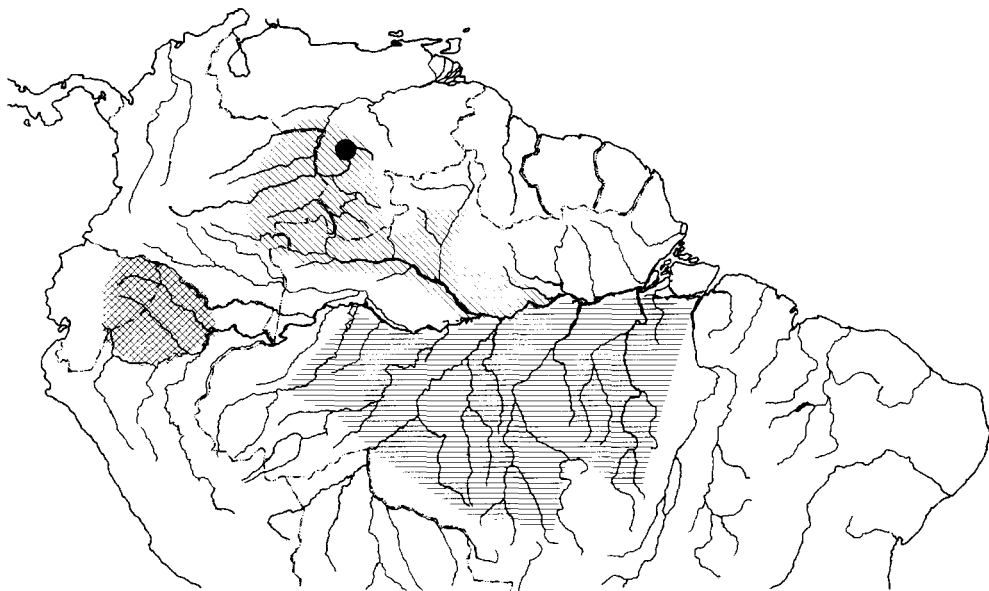
FIGURE 1.   Distribution of the three species of the genus *Heterocercus*: the Yellow-crowned Manakin (*H. flavivertex*) in diagonal hatching, Flame-crowned Manakin (*H. linteatus*) in horizontal hatching, and Orange-crowned Manakin (*H. aurantiivertex*) in cross hatching. The location of the study site, Campamento Camani on the Rio Ventuari, Venezuela, is shown by the dot.

ertex on the Upper Rio Ventuari, Venezuela to address this lack of natural history data for the genus.

LOCALITY AND METHODS

The observations were conducted at Campamento Camani (formerly called Junglaven Lodge) on the upper Rio Ventuari, Territorio Federal Amazonas, Venezuela (~ 5°08'N, 66°15'W; 200 meters; Fig. 1). The locality is an area of mixed seasonally flooded varzea forest, white-sand woodland, open white-sand savanna, and terra firma forest. Over 300 species of birds have been observed at this site (Zimmer and Hilty, unpubl. data).

Observations were made at Campamento Camani from 10–11 March 1990 and 22 March–20 April 1990. At the beginning of the observations, nothing was known about the vocalizations, behavior, or natural history of *H. flavivertex*. Because of this complete lack of information and the tremendous diversity of the avifauna at the site, Prum and Kaplan spent 10–11 March and 22 March–5 April 1990 searching for *H. flavivertex*, frequently in inappropriate habitats. On 6 April, Prum and Kaplan identified the first territorial male *flavivertex* and began structured observations of this individual. A second

territorial male *flavivertex* was located on 11 April. Structured observations of both males were conducted daily until 20 April (by which time vocalization and territorial attendance had de-
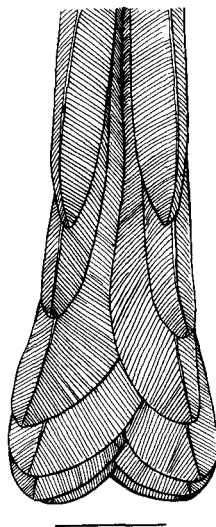

FIGURE 2.   Ventral view of the rectrices of a male *Heterocercus flavivertex* (USNM 326942). The outer rectrices (6-6) are less than half the length and width of the inner rectrices (1-1). The feather rachi are not stiffened. Scale bar equals 10 mm.

clined significantly). Additional observations were made at the same locality by Kaplan and Pierson from 16–22 February 1992.

Mist nets were deployed on 7–9 April 1990, and four *flavivertex* were caught and banded with distinctive color combinations. Three banded individuals (Green-White, Yellow-Blue, and White-Red) were females or predefinitive males and were never observed again. A territorial male in definitive plumage was banded Orange-Orange. The second territorial male was not banded to minimize disturbance at that display site.

A total of 91.3 hours of structured observations of the two territorial males were made during the observation period. Focal individuals were observed with binoculars and without blinds. Observations were recorded using five minute sampling periods. The following data were recorded for each sampling period: presence of the male, and frequency of exits and entrances, position and height of the perch, the number of perch changes, the number of the various vocalizations and displays, intraspecific encounters and aggressive flights, preening, sunbathing, foraging and type of food item, and method of foraging. Rare behaviors may have been underestimated during the initial observation days before the behavioral repertoire was better known. Daily observations started by 06:30 and continued until male territorial attendance and vocal activity ceased (between 11:00 and 14:00). Additional afternoon observations (14:00 to 17:00) were made on 6 observations days, but they indicate reduced territorial and display activity.

Foraging observations of male and female *flavivertex* were made opportunistically throughout the observation period. Observations of territorial males were more thorough because of additional observations in their display territories.

Over 6 hours of acoustic tape recordings of vocalizations were made using a Sony TCM-5000 and Sennheiser ME-80 and ME-88 microphones. Over 4 hours of 8mm video tape recordings were made using a Sony Sports Handycam CCD-SP9. Vocalizations will be deposited at the Cornell University Library of Natural Sounds. Recordings are referred to here by the original ROP tape reference numbers which give the tape number and side.

Vocalizations were analyzed using Canary 1.2 from the Cornell University Library of Natural Sounds on a Macintosh Computer. Measurements reported below are from specimens of the American Museum of Natural History (AMNH), New York, and Paris Museum of Natural History (PM). Additional observations were made of study skins in the Collecíon Phelps, Caracas, Venezuela. Museum specimens of *flavivertex* in the Collecíon Phelps were examined to investigate reproductive seasonality (this is the only significant collection of *flavivertex* with any information on reproductive condition). A drawing of the gonads was made on the data label of each specimen at the time of preparation. Males with testes > 5 mm long, and females with ovaries > 5 mm or follicles > 2 mm were considered to be in breeding condition. The single nest collected was deposited at the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Illustrations of the displays were prepared by Carolyn Wooster from video tape recordings and study skins borrowed from the National Museum of Natural History, Smithsonian Institution, Washington, DC.

RESULTS

MORPHOLOGY

Male *flavivertex* have deep green upperparts with a yellow central crown stripe. The underparts blend from warm cinnamon on the undertail coverts to dark chestnut on the upper breast. The throat is bright white with elongate side plumes. Females lack the crown stripe and have a drabber but distinct gray throat patch. Both sexes have a dark gray check patch that contrasts with the green upperparts and light throat. Some males with reproductively active testes have a female-like, predefinitive plumage (specimens in Collecíon Phelps). Time of acquisition of definitive male plumage is unknown.

The tail of both sexes is an unusual shape for manakins (Fig. 2). The outer rectrices (6-6) average less than half the length of the longest inner rectrices (1-1) (Table 1), and are much narrower. The sexes show little size dimorphism, except that males have significantly longer wings than females ($P < 0.002$; Table 1).

Few body mass data are available for this species. The three female/predefinitive male individuals banded weighed 21.5, 21.5, and 18.3 g, respectively. A single definitive plumage male (OO) weighed 21.3 g. Willard et al. (1991) reported no sexual dimorphism in mass in a sample of five males ($\bar{x} \pm SD = 21.5 \pm 1.9$ g) and

TABLE 1. Measurements of study skin specimens of the genus *Heterocercus*. There is no significant sexual size dimorphism for any measurement other than wing length. *H. flavivertex* and *H. linteatus* show significant male-biased sexual size dimorphism for wing length (flat) at the $P < 0.01$ level (**). Samples of *H. aurantiivertex* are too small to be significant but show similar levels of dimorphism.

	Bill from tip to nostril	Bill width	Tarsus	Central rectrices (1-1)	Outer rectrices (6-6)	Wing length (flat)
Heterocercus flavivertex						
Male mean ± SD	8.45 ± 0.29	8.28 ± 0.49	15.15 ± 0.44	50.5 ± 1.57	21.1 ± 1.64	86.8 ± 1.67**
n	16	16	16	16	16	16
Range (wing only)						85.0–90.5
Female mean ± SD	8.47 ± 0.28	8.71 ± 0.60	14.97 ± 0.57	50.4 ± 2.25	21.8 ± 1.97	81.2 ± 2.12**
n	14	14	14	14	14	13
Range (wing only)						78.0–83.0
Heterocercus linteatus						
Male mean ± SD	8.34 ± 0.29	8.17 ± 0.64	15.42 ± 0.73	52.7 ± 2.16	24.4 ± 1.49	88.4 ± 2.00**
n	10	10	9	10	10	10
Range (wing only)						85.0–90.0
Female mean ± SD	8.20 ± 0.34	8.51 ± 0.70	15.69 ± 0.46	51.7 ± 2.02	25.6 ± 1.63	80.78 ± 2.25**
n	7	7	7	7	6	7
Range (wing only)						78.0–84.0
Heterocercus aurantiivertex						
Male mean ± SD	8.97 ± 1.05	12.07 ± 0.70	14.67 ± 0.15	48.5 ± 1.80	25.3 ± 0.57	85.0 ± 1.50
n	3	3	3	3	3	3
Range (wing only)						83.5–86.5
Female mean ± SD	9.25 ± 0.07	11.55 ± 0.07	14.45 ± 0.78	48.0 ± 1.41	23.3 ± 2.47	81.0 ± 0
n	2	2	2	2	2	2
Range (wing only)						81–81

TABLE 2. Frequency of vocalizations and displays of the Yellow-crowned Manakin (*Heterocercus flavivertex*) in Território Amazonas, Venezuela.

	Observation hours	Observation days	% territorial attendance[a]	*Weeee-pítch-ooo* call[b]	*Weeee* call[b]	Tail-shiver display[b]	Aggressive flight and chatter call[b]
All observations	93.1	19	73	3.48	3.0	0.13	0.66
Peak activity[c]	30	4	84	5.76	3.72	0.13	0.60
Low activity[d]	9	3	78	0.34	0.01	0	0.15

[a] Territorial attendance is reported as the % of observation periods when a male was observed on territory.
[b] Displays and vocal frequencies are reported as average number of observations per hour of observation.
[c] Peak activity frequencies were calculated from data collected on four mornings (07:00–12:00) between 11–14 April 1990.
[d] Low activity frequencies were calculated from data collected on three mornings between 16–20 April 1990.

3 females ($\bar{x} \pm$ SD = 21.7 ± 1.3 g) from southern Amazonas, Venezuela.

DISTRIBUTION AND HABITAT

Heterocercus flavivertex is distributed in the Rio Negro drainage of eastern Colombia, southern Venezuela and Brazil, the Upper Rio Orinoco drainage of Venezuela as far north as the Rio Capanaparo, Estado Apure, Venezuela (Goodwin and Lentino 1992; specimen Colleción Phelps, Caracas), and on the left bank of the Amazon in Pará, Brazil (Fig. 1; Snow 1979, Haffer 1986, Ridgely and Tudor 1994). All known localities are below 300 m in elevation. The Colleción Phelps includes 104 study skins from 12 localities along rivers throughout Territorio Amazonas, Venezuela, representing essentially every locality sampled in Amazonas within appropriate habitat.

Heterocercus flavivertex was observed at Campamento Camani in seasonally flooded varzea forest of the Rio Ventuari and its tributaries, in scrubby woodlands found on white sand soils that border the varzea, and in seasonally flooded riparian forest along blackwater streams and oxbow lakes. Other sources report *flavivertex* in similar habitats in other parts of its range (Hilty and Brown 1986, Ridgely and Tudor 1994). The sites at Campamento Camani were characterized by a rather short canopy (~ 8–15 m) and thick undergrowth of vines, palms and small trees. *H. flavivertex* was never observed in terra firma forest in this area. A few individuals were observed foraging in small shrubs in open savanna that border the white-sand woodlands. These individuals apparently were foraging opportunistically at the edge of their preferred habitat.

MALE TERRITORIALITY

Two male *flavivertex*—Orange-Orange (OO) and unbanded (UB)—were observed defending non-resource-based territories in varzea forest for a period of two weeks. Territoriality was inferred by consistent attendance in an area over a number of days. The two males were in attendance on their territories during 73% of the 1,096 5-min observation periods on 19 bird observation days (Table 2). Each territory included a core area 10 m in diameter where males were observed > 75% of the time in attendance. The entire area of perch sites where territorial defense (i. e., vocalization or display) was observed was approximately 20 m in diameter.

Each male territory was solitary—i.e., completely out of hearing distance from other male *flavivertex* territories. The two territories observed were separated by ~250 m of relatively disturbed habitat without any intervening males. However, both territories were on the edge of a large expanse of continuous habitat that lacked nearby territories. Twenty-two months later during February 1992, OO and an unbanded male occupied the same two territories and were observed using the same calling perches. No additional intervening male territories were found at that time.

Males perched on tree branches and horizontal vines at heights of 3–6 m. Males defended territories by vocalizing and performing aggressive flight displays (see below). Male territories included a few fruit trees, but males frequently left the territory to forage. Female-plumaged birds were not observed in the territories for more than a few seconds.

VOCALIZATIONS

Male *flavivertex* have a repertoire of at least five distinct vocalizations with several minor variations. The full advertisement call is a loud, three-note, whistled *weeee-pítch-ooo* (Fig. 3) approximately 3 sec long. The first note of the call rises slowly from ~ 4.5 to 5.25 kHz over 1.6 sec. After
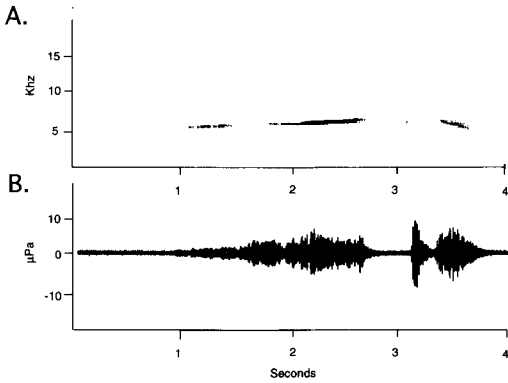
A.

B.

FIGURE 3. Spectrogram (above) and waveform (below) of the full advertisement call, *weeee-pítch-ooo,* of *Heterocercus flavivertex* (ROP-1990-V1). Khz: kilohertz (frequency); mPa: micropascal (pressure).

a 0.6 sec pause, the second note rises rapidly from ~ 4.5 to 6 kHz over 0.2 sec. Then, after a very brief pause of < 0.1 sec, the third note descends slowly from 6 to 3.8 kHz over ~ 0.8 sec. The amplitude, or volume, of the call increases dramatically in the first note of the call, peaks in the second note, and drops off gradually in the third (Fig. 3), giving the call a dramatic, punctuated, or hiccuping cadence. The erect display posture associated with this vocalization is described below (see Display Behavior).

Sometimes the full advertisement call included a double introductory *weeee* note. Males also gave a partial advertisement call. This call consists of a single rising *weeee* note that is identical to the initial note of the full advertisement call but typically of lower volume. Males occasionally give a double version with two *weeee* notes repeated.

Males give an emphatic *weer-weer . . . weer* chatter call during aggressive interactions with other individual *flavivertex* and occasionally other species. The aggressive chatter call is characterized by three to six sharp, squeaky notes that are successively lower in volume and frequency. Each note is composed of two strong harmonics that rise rapidly in frequency over the first 0.06 sec and then drop slowly in frequency over the last ~ 0.15 sec (Fig. 4). Each subsequent note in the series is slightly shorter and lower in amplitude and frequency.

Males also give a dry, emphatic *chíp* as they fly from a perch immediately following the tail-shiver display (see below). The *chíp* is a short,

< 0.1 sec note that descends from 8.3 to 5.6 kHz (Fig. 5A).

Two additional vocalizations—a querulous *kweip* and a loud *keek*—were heard on a few occasions immediately following performances of the tail-shiver display. The *kweip* note was recorded once. It consists of three very short syllables in quick succession: 5.9 kHz for 0.15 sec, 6.33 kHz for 0.05 sec, and 5.5 kHz for 0.05 sec (Fig. 5B). The *keek* note was not recorded.

DISPLAY BEHAVIOR AND MECHANICAL
SOUND PRODUCTION

Three conspicuous displays were observed. Male *flavivertex* perform a stylized, erect display posture while giving the full advertisement call—*weeee-pítch-ooo* (Fig. 6A). The male perches very erect with its head pulled in and the beak upraised, exposing the white throat patch. During the initial *weeee* note, the male gradually opens its beak wider and wider. At the beginning of the explosive *pítch-ooo* notes, the male throws his beak open very broadly, exposing the bright yellow tongue and gape. At the same time, the wings and body twitch conspicuously with physical exertion, as they do in the Screaming Piha (*Lipaugus vociferans,* Cotingidae; Snow 1982) when it calls.

Territorial males give the *weeee-pítch-ooo* and *weeee* calls as advertisement and territorial defense vocalizations. These vocalizations were given an average of 3.48 and 3.0 times per hour, respectively, across all observation days (Table 2). Calling frequency varied from 5.76 *weeee-pítch-ooo* and 3.72 *weeee* calls per hour during the morning (07:00–12:00) on four of the most active days, to 0.34 and 0.01 calls per hour, respectively during the mornings of three of the last observation days (Table 2). The highest calling frequency recorded was 7.6 *weeee-pítch-ooo* calls per hour on one morning.
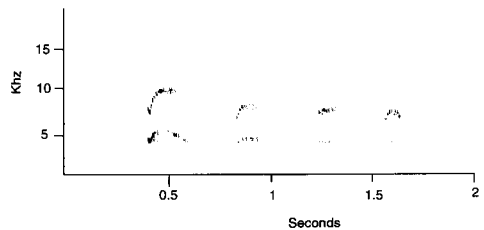

FIGURE 4. Spectrogram of the aggressive chatter call, *weer-weer . . . weer,* of *Heterocercus flavivertex* (ROP-1990-7A).
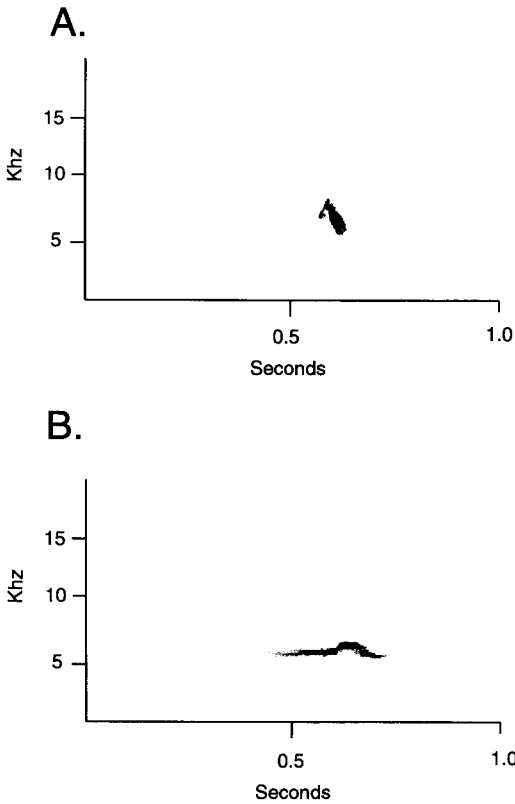
A.

B.

FIGURE 5. Spectrograms of: (A) the *chíp* call (ROP-1990-6B) and (B) the *kweip* note (ROP-1990-6B) of *Heterocercus flavivertex*.

In the conspicuous tail-shiver display (Fig. 6B), a male perches on a branch with the body horizontal and the tail cocked at a nearly right angle above its back. The white throat is erected into a puff, and the wings are folded against the body. The male moves the tail forward and back over approximately 15°, and simultaneously rocks its body slightly in the opposite direction, producing a rapid, syncopated "shivering" movement. The male then flies conspicuously from the perch, holding its entire body horizontal, flapping its wings very deeply, and giving an emphatic *chíp* call. An 8 mm video tape recording of a single tail-shiver display documented four rapid tail and body twitching movements in less than one second.

The tail-shiver display was observed twelve times on five different observation days between 07:15 and 15:55, for a total frequency of 0.13 displays per observation hour. The peak display frequency was 2.76 performances per hour between 12:00–14:10 on a single observation day. The performance of the display was usually preceded and followed by an increase in advertisement vocalization. Usually, the male was observed looking intently off into the forest immediately before performing the display. These displays may have been directed toward an unseen female.

On one occasion, J. Pierson saw an elaborate flight display from a trail through open savanna bordering on white-sand woodland approximately 2 km from the focal male territories. Following a series of aggressive chatter calls by one or two unseen individuals, a male *flavivertex* flew rapidly and rather vertically from one side of a trail up about 15–20 m above the woodland canopy. It then flew horizontally in a semicircle about 10–12 m in diameter, and dropped abruptly down into the woodland on the other side of the trail. The entire flight took between 6 and 8 sec. No other flight displays were observed. However, an unusual whooshing sound was heard at least 3 or 4 times in the subsequent 20-min period. The sound was a high-pitched, ~1 sec, down-slurred *whoosh*.

Prum or Kaplan did not observe this flight display. However, Prum tape recorded a sound in the territory of male UB that is strikingly similar to the sound later described by Pierson. On that occasion, the male performed a tail-shiver display and flew off the perch giving the sharp *chíp* note. One and a half seconds after the *chíp*, a descending *whoosh* sound was recorded (Fig. 7). The sound is 0.75 sec long and contains two portions. The first part is a continuous *whoosh* that steadily increases in amplitude. It is followed immediately by a short thud that punctuates the end of the sound. The recorded *whoosh* sound is reminiscent of an arrow flying by and hitting a target; it may be produced by the bird flying very fast and stopping in flight suddenly. The sound was not noticed at the time of recording, but is actually greater in amplitude (louder) on the recording than the *chíp* note that was recorded under excellent conditions.

The association of this *whoosh* sound with a tail-shiver display supports the conjecture that it is a mechanical display sound. These observations also indicate that *flavivertex* may have two flight displays. This mechanical *whoosh* flight display is apparently distinct from the above-
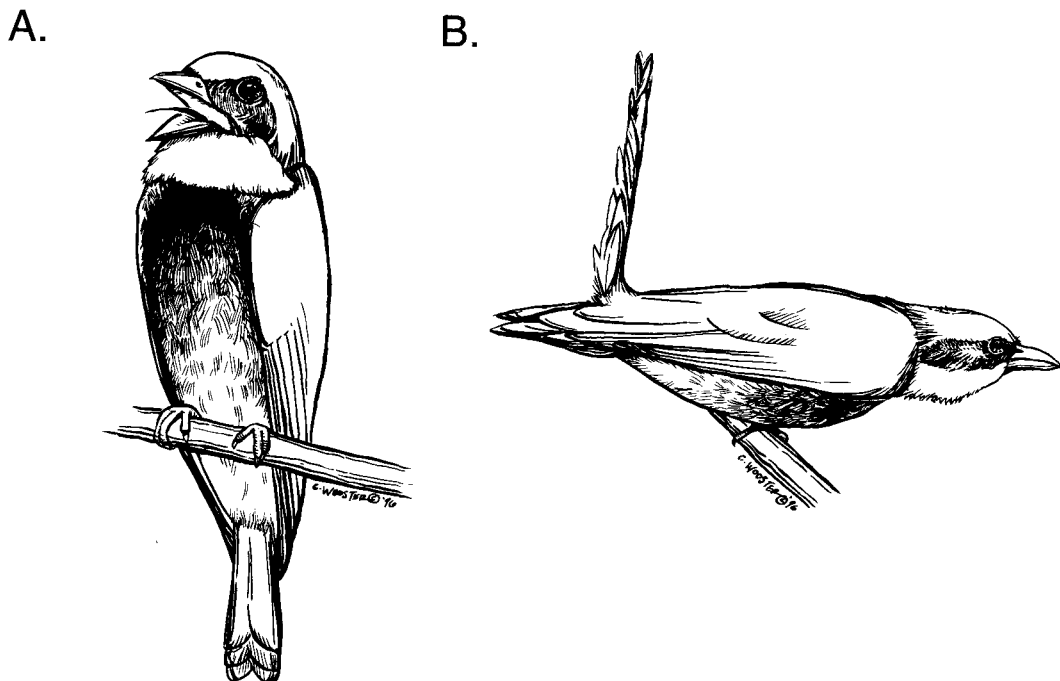
A.   **B.**

FIGURE 6.   Display elements of *Heterocercus flavivertex*. (A) the erect posture. (B) the tail-shiver display. See text for details.

the-canopy display, since no whooshing noises were heard during the observation of the above-the-canopy display, and no above-the-canopy flights were observed when the *whoosh* sounds were heard. Further, the possible recording of the *whoosh* was made 1.5 sec after male UB performed a tail-shiver display and flew from a perch in the territory. This is not enough time for the male to perform the 6–8 sec long above-the-canopy flight display.

AGGRESSIVE INTERACTIONS

The chatter vocalization is apparently given when a male observes a conspecific in the vicinity of its territory. Typically, the resident male would suddenly peer intently at the surrounding vegetation and then suddenly fly from the perch giving the aggressive chatter call ($n = 59$). Aggressive flights were observed an average of 0.6 times per observation hour (Table 2). Males were so vigilant that on all but one occasion, the second bird was never seen or heard by the observers. In several cases, males directed aggressive flights and chatter calls at individuals of other species (e.g., *Bucco tamatia*).

NESTING

A female *flavivertex* was observed constructing a nest on 3 April 1990 on Caño Guayahe, a small tributary on the right bank of the Rio Ventuari that is several kilometers upstream from Cam-
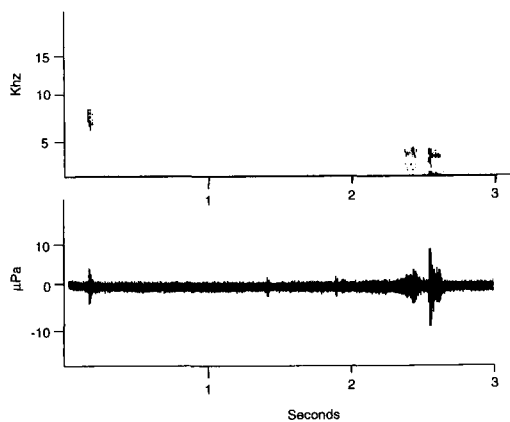

FIGURE 7.   Spectrogram (above) and waveform (below) of a *chíp* display call (left) and a probable mechanical *whoosh* sound (right) (ROP-1990-7A).

TABLE 3.   Observations of foraging behavior and estimates of diet composition in male *Heterocercus flavivertex*. The estimate of diet composition includes seed regurgitation events as indirect observations of fruit foraging events.

	Fruit	Arthropods	Unknown	Total foraging events	Seed regurgitation
Observations	11	70	19	100	49
Frequency hr^{-1}	0.12	0.76	0.20	1.09	0.53
Estimated percent diet composition	40	46	14	—	—

pamento Camani. The nest was a hanging cup built in a fork of the lowest, descending branch of a 15 m tall, broadleafed tree on the edge of Caño Guayahe, which was approximately 8 m wide at this site. The nest was placed 2 m above the surface of the water on the lowest point of the branch. The nest was not within a male territory. The female *flavivertex* was observed adding stiff, thin fibrous twigs to the nest, and shaping the interior of the nest by pressing the nest cup with her breast. The nest was observed again two weeks later. It had been abandoned soon after the first observations and was then collected (USNM 48163).

The collected nest may have been incomplete when abandoned. The nest cup is transparent, and measures 57.3 × 45.1 mm at the widest and narrowest exterior dimensions, and 22.6 mm deep. The internal depth of the nest cup is 15 mm. The branches supporting the nest are uniformly 5 mm in diameter, and the center of the nest cup is 46 mm from the fork of the branch. The nest cup is composed of a variety of plant fibers including rootlets, small twigs, and a large number of wiry, round, grass-like fibers. Some plant fibers are very long and are bent and woven around into the nest cup without breaking. The edges of the nest are attached to the branches by masses of spider web.

DIET

Heterocercus flavivertex were observed foraging on a variety of fruits and invertebrates. Both sexes were observed foraging at fruiting trees in varzea forest with other frugivores (including Black-headed Parrot *Pionites melanocephala*, Cuvier's Toucan *Ramphastos cuvieri*, Many-banded Araçari *Pteroglossus pluricinctus*, Spangled Cotinga *Cotinga cayana*, Pompador Cotinga *Xipholena punicea*, Black Manakin *Xenopipo atronitens*, and Golden-headed Manakin *Pipra erythrocephala*). These fruit tree species included members of the Melastomataceae, Lauraceae, and Rubiaceae (identifications of herbarium specimens collected is pending).

Male *flavivertex* were often observed foraging in and around their territories. In total, an average of 1.1 foraging events per hour were observed (Table 3). In 19 instances, the food items could not be identified. On 11 occasions, males were observed foraging on fruits, which they seized in the bill during aerial sallies. In addition to these actual foraging events, males were observed regurgitating seeds while perched in the display territories (Table 3). Regurgitated seeds varied in size by a couple orders of magnitude from < 1 mm to > 20 mm in length.

On 70 occasions, we observed males eating invertebrates. Invertebrate foraging maneuvers included aerial sallies, gleaning from branches and leaves in flight, and, rarely, gleaning from branches while perched. Males pursued prey in very active aerial sallies at all heights in the forest from 1–10 m. Occasionally, individuals produced loud bill snaps during these aerial sallies. Most invertebrate prey were flying insects too small to identify, but prey included a caterpillar 4 cm long and a 2 cm long spider. A male was once observed foraging for prey by hovering in front of a web of an orb-weaving spider. The maneuver was repeated five times in quick succession without any apparent prey capture.

PREENING AND SUNBATHING

The predominant activity of males on territory was preening. Males were observed preening in 297 of 1,096 5-min observation periods, or 37% of the 798 observation periods in which males were known to be present on territory. Males preened by running the beak through their feathers. They also scratched themselves with the leg raised over the open wing. Preening frequency was consistent throughout the day. On one occasion, male OO was conspicuously wet when it

returned to its territory, having apparently bathed in standing water.

Territorial males were observed sunbathing on 27 occasions (an average of 0.26 times per hour). During sunbathing, males perched between 5–10 m high in a patch of sun, and spread and angled the wings and tail so that their upper surfaces were exposed directly to the sun. Frequently, the males cocked their tails or lay prostrate against a perch to expose themselves to the sun efficiently. These postures were so conspicuous and stereotyped that they were initially interpreted as potential display elements. Repeated observations, however, confirmed these postures as hygiene behavior. Bouts of sunbathing were observed at various times from 08:15 to 16:05 and lasted from 10 to 120 sec. Immediately after sunbathing, males returned to calling perches in their territories and began preening vigorously.

SEASONALITY

The observation of nest construction by a female on 3 April 1990 and male territoriality and display behavior between 6–23 April 1990 indicate that *H. flavivertex* were actively breeding during this month. During April 1990, male territorial activity and frequency of vocalization dropped dramatically (Table 2), indicating that at this site the end of the reproductive season may have been approaching. For example, the frequency of *weeee-pítch-ooo* calls averaged 5.76 calls per hour during five mornings between 11–14 April, whereas the frequency of this vocalization by these same individuals was 0.32 calls per hour during three mornings between 16–20 April (Table 2). Additional unstructured observations at the site by Kaplan in 1992 indicate that male vocal activity was even greater in mid-February than in April.

Specimens from different years and localities throughout Amazonas, Venezuela indicate that males are reproductively active in February, March, and May ($n = 36$), and have smaller testes in January, July, and August ($n = 6$). A few male specimens showed decreased testes size in May ($n = 4$). Female specimens had enlarged ovaries in late February and March ($n = 4$), but other specimens showed smaller ovaries in January, February, March, May, and August ($n = 12$). All reproductively active specimens of both sexes fall between 11 February and 19 May, but no specimens with gonad data exist for April or June, or during the rainy season from September through December. Willard et al. (1991) reported enlarged testes and ovaries in specimens from southern Territorio Amazonas, Venezuela during February, March and April, and one female individual with small gonads in February.

The Amazonas region of Venezuela is subject to strongly seasonal rainfall, with prolonged dry seasons from December to April and rainy seasons from April until November (Hilty and Brown 1986). These limited behavioral observations and museum specimens indicate that the breeding season of *H. flavivertex* in Amazonas, Venezuela occurs during the dry season, probably beginning by February and ending toward the end of April or May.

DISCUSSION

BREEDING SYSTEM

Our observations indicate that *Heterocercus flavivertex* has a display polygyny breeding system, like most other behaviorally known manakin species. Males occupy small, non-resource-based defense territories and perform elaborate courtship displays. Unlike other non-cooperative manakins species, in which male display territories are aggregated into groups of adjacent, neighboring males, the territories of male *flavivertex* are apparently solitary. Both males observed defended territories that were out of acoustic range of other males.

This apparent, complete dispersion of male territories could be hypothesized to be caused by low population density (Bradbury 1981). Few data are available on *flavivertex* population density, but *flavivertex* appears to be relatively common in appropriate habitat at this and other localities (Hilty and Brown 1986). *H. flavivertex* were collected regularly during expeditions to localities throughout Territorio Amazonas by the Colección Phelps. Evidence from populations of the White-bearded Manakin *Manacus manacus* indicate that lek size can change with population density, but other aspects of lek territoriality, such as territory size and intermale distance, remain unchanged (Olsen and McDowell 1983).

The behavior of male *flavivertex* supports the conclusion that male territories are solitary for social rather than demographic reasons. Male *flavivertex* responded extremely aggressively to any conspecific individuals near their territories. Aggregated display territories with multiple adjacent males require at least a moderate amount

of social tolerance among males. Male *flavivertex* are strikingly different from other manakins in that they show complete intolerance to conspecific males. This indicates that solitary display territories are typical of the breeding system of this species. Interestingly, a similar, solitary display territoriality has been observed in the Orange-crowned Manakin *H. aurantiivertex* on the Rio Napo, Ecuador (Prum, unpubl. data). Although more data are required to determine whether *flavivertex* territories are uniformly distributed or clumped within the habitat, *Heterocercus* territories are apparently distinct from other behaviorally-known species of manakins in that territorial males are physically and socially isolated from other territorial males.

Prum (1994) hypothesized that solitary display territoriality in *Heterocercus* is evolutionarily derived from the dispersed lek that is plesiomorphic, or primitive, to the manakin family. The solitary advertisement system has apparently evolved through the derived loss of male social aggregation. Prum (1994) proposed that this breeding system be called a "solitary lek" since: (1) solitary leks, in this and possibly other instances, may be historically derived from traditional, aggregated classes of lek territoriality and (2) solitary leks share the most important feature with traditional, aggregated leks—that is, males defend non-resource-based territories for polygynous advertisement.

NESTING

The nest of *flavivertex* is typical in architecture, composition, position, and size to other manakin species (Snow 1962, Skutch 1969, Wetmore 1972, Foster 1976, Dujardin 1987). Some manakin species build a flimsy cup that is transparent enough for the contents to be visible from below (e.g., *Pipra* and *Manacus*), similar to the possibly incomplete *flavivertex* nest collected. In contrast, the Long-tailed Manakin *Chiroxiphia linearis*, White-fronted Manakin *Lepidothrix serena*, and Blue-crowned Manakin *L. coronata* build a more substantial cup that is heavily adorned with moss or hanging dry leaves (Skutch 1969, Wetmore 1972, Foster 1976, Dujardin 1987). The use of spider webs and long plant fibers by *H. flavivertex* is very similar to *Manacus manacus* (Snow 1962). Nests of various manakins are also commonly placed over streams but these streams are usually smaller than the river where the *flavivertex* nest was found. Male *flavivertex* were not observed

in association with any nests, and apparently females perform the parental care duties alone.

VOCAL AND DISPLAY BEHAVIOR

The vocal and display repertoires of *Heterocercus flavivertex* are unlike those known in other genera and species of the family. The dramatic advertisement call is unlike any vocalization known from other manakin genera, but may be similar and homologous to the advertisement call of *H. linteatus*, described by Sick (1993:501) as *pit-eew*. Interestingly, the advertisement call of *H. aurantiivertex* is completely different from the two other species in the genus (Prum, unpubl. data). The *aurantiivertex* advertisement call is a meandering, chattering trill of sharp chip notes. This vocalization is a lengthened version of the homologous aggressive chatter calls of *flavivertex* but differs in function. Depending on which type of advertisement call is primitive to the genus, the aggressive chattering call either evolved secondarily into a novel advertisement call in *aurantiivertex*, or a chattering advertisement call was replaced by a derived, whistled advertisement call in a putative common ancestor of *flavivertex* and *linteatus*.

The erect display posture of *flavivertex* has evolved in direct association with the advertisement call (Fig. 6A). The visual and acoustic components of this complex display are interrelated and inseparable. In many regards, this display is similar to the loud vocal advertisements in the Screaming and Rufous Pihas (*Lipaugus*) or the Capuchinbird (*Perissocephalus tricolor;* Cotingidae; Snow 1982).

The tail-shiver display of *flavivertex* is unique (Fig. 6B). No other known manakin display includes a cocked-tailed, horizontal posture, a syncopated shivering movement, or a departure from a perch with *chip* note. The "wing-shiver" display of the *Pipra aureola* clade features a horizontal posture with the tail-cocked but the wings are shivered rapidly rather than the body and tail rocking rapidly back and forth (Snow 1963a, Schwartz and Snow 1978, Robbins 1983). It is possible, however, that the horizontal component of the *flavivertex* tail-shiver display is homologous with the horizontal posture shared by species of *Pipra* (Prum 1990a; character 4). If so, this behavioral homolog has been elaborated independently in various displays within the two genera. The *flavivertex* tail-shiver display may be similar to an undescribed display of *Chiroxiphia*

linearis (D. B. McDonald, pers. comm.), but any such similarities are probably convergences given the phylogenetic relationships of these genera to other manakins which apparently lack such a display.

According to Sick (1993), *linteatus* also erects its white throat patch, as *flavivertex* does in the tail-shiver display. It is not known, however, whether *linteatus* or *aurantiivertex* perform the tail-shiver display, or any behavioral homolog. In some other manakin species, unusual tail morphologies are associated with specific display elements in which they are prominently featured. The tail-shiver display of *flavivertex* is a plausible explanation for the evolution of this unusual morphology in *Heterocercus*. The occurrence of identical tails in all three species of the genus suggests that a homolog of the tail-shiver display is also performed by *linteatus* and *aurantiivertex*.

The *flavivertex* above-the-canopy flight display is an impressive behavior that remains poorly known. A similar flight display, in which males fly as high as 100 m above-the-canopy, has recently been observed in *H. aurantiivertex* in Departemento Loreto, Peru (J. Alvarez and B. Whitney, pers. comm.). Apparently, this flight display is a behavioral homolog shared by these two species. The display probably evolved in the common ancestor of the genus *Heterocercus* and is probably performed by *linteatus*. Interestingly, males of all *Heterocercus* species have significantly longer wings than females, even though they are not sexually dimorphic in other measurements including tail shape (Table 1). The longer male wing length may have evolved as a consequence of selection for demanding flight performance in aerial displays. A positive association between wing length and flight displays is predicted by the general, positive correlation between wing length and flight performance in birds (Greenewalt 1962).

Another *flavivertex* flight display may be associated with the production of a mechanical sound. *H. aurantiivertex* does make a mechanical sound in association with a flight display (J. Alvarez and B. Whitney, pers. comm.). These mechanical sounds could be produced by either the wings or the tail. However, all manakin species that produce mechanical sounds have sexually dimorphic wings feathers (Prum, unpubl. data). The sexual dimorphism in wing length and the lack of sexual dimorphism in tail shape in *Heterocercus* are consistent with the hypothesis that the wing is responsible for these mechanical sounds (Table 1).

Elsewhere in manakins, only species in the genus *Corapipo* perform elaborate, above-the-canopy flight displays with synchronized vocalizations and mechanical wing sounds (Davis 1982, Prum 1986, 1990a). However, any similarities between the displays of *Heterocercus* and *Corapipo* are convergent and evolutionarily independent of one another. The only complete phylogenetic hypothesis for the manakins indicates that *Heterocercus* is closely related to the genus *Pipra (sensu stricto,* excluding the *serena* group), whereas *Corapipo* is most closely related to *Masius* and *Ilicura* (Prum 1990a, 1992). These conspicuous displays probably serve a convergent advertisement function in the two genera.

DIET

A crude estimate of diet composition based on observations of foraging and seed regurgitation indicate that arthropods are a major component of the diet of *H. flavivertex* (Table 2). These data are skewed by many factors. For example, fruit resources are generally patchy and probably lower in density within male territories where many of these observations were made. Also, males certainly foraged opportunistically within their territories on arthropod resources which are typically more uniformly distributed than fruit. Arthropods, however, are clearly an important food resource for *flavivertex*. Although comparable data do not exist for other manakin species, arthropod foraging was observed more than an order of magnitude less frequently than fruit foraging in all previous observations of 15 other species of manakins throughout the Neotropics (R. O. Prum, pers. observ.). Interestingly, observation of foraging by male *H. aurantiivertex* indicate a similar, large component of arthropods in the diet.

The striking differences in the diets of *Heterocercus* from those of other manakins may be related to the evolution of some of the other differences in morphology, habitat, and social behavior. *Heterocercus* species have a longer, narrower bill than do other manakins. This feature is probably derived within the genus and may be an adaptation to insect foraging. *Heterocercus* species live in seasonally flooded forest habitats, which are not preferred by other manakin species. The shift in the diet composition may be related to the derived occupation of the

novel habitat within the family. Lastly, many proximate ecological models hypothesize a relationship between lek size characteristics and resource distribution (Emlen and Oring 1977, Bradbury 1981, Bradbury and Gibson 1983, Foster 1983, Beehler and Foster 1988). The novel diet in *Heterocercus* may influence the distribution of reproductive resources in the genus and may have resulted in the evolution or strategic adoption of a solitary lek breeding system. Insect foraging should lead to more uniform distribution of reproductive resources and thereby to reduced home range size and home range overlap, which can result from clumped resources. Both of these factors would favor reduced lek size and increased male dispersion in either the female choice (Bradbury 1981) or hot-spot (Bradbury and Gibson 1983) models of lek determination. Alternatively, the novel solitary lek system may have evolved by sexual selection on genetic variation for male social behavior itself (Queller 1987, Prum 1994). Additional comparative research on diet and social behavior of *Heterocercus* and other manakins may help to further test associations between ecology, sexual selection, and social behavior in the family.

TAXONOMY

From the late 19th century (Sclater 1888) until recently (Snow 1975, 1979), *Heterocercus* has been viewed as an aberrant genus within the manakin family, based on its larger size, atypical plumage, and body and bill proportions. Most recently, Prum (1990b, 1992) removed six aberrant genera from the manakin family, but strongly confirmed the placement of *Heterocercus* within the piprids as the closest relatives of the type genus *Pipra*. These behavioral observations further document that *Heterocercus* shares the derived lek social behavior, display polygyny, and nest architecture that is typical of other sexually dimorphic manakins, and confirms its placement within the manakin clade.

ACKNOWLEDGMENTS

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