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DISPLAY BEHAVIOR, FORAGING ECOLOGY, AND SYSTEMATICS OF THE GOLDEN-WINGED MANAKIN (*MASIUS CHRYSOPTERUS*)

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ABSTRACT.—The displays and foraging behavior of the Golden-winged Manakin (*Masius chrysopterus*: Pipridae) were observed at two sites in western Ecuador from May to July 1985. *Masius* foraged both solitarily and with multispecies foraging flocks, and fed on fruits of 10 plant species from four botanical families. Male *Masius* occupied 30–40-m diameter display territories arranged in dispersed leks. Males defended territories through frequent advertisement calling, and performed displays on fallen logs and exposed buttress roots within each territory. Courtship display elements included a complex log-approach display, a chin-down display, and a side-to-side bowing display. Pairs of males performed coordinated log-approach and side-to-side bowing displays but the function of these coordinated behaviors was not determined. A phylogenetic analysis of display behaviors strongly indicates that *Masius* is the sister-group to the genus *Corapipo* and that *Ilicura* may be the sister-group to these two genera. These conclusions are partially corroborated by morphological and biochemical evidence. *Received 5 Aug. 1986, accepted 27 Feb. 1987.*

RESÚMEN.—Los comportamientos de alimentación y cortejo del saltarín ali-dorado (*Masius chrysopterus*: Pipridae) se observaron en dos lugares en Ecuador occidental en los meses de mayo a julio de 1985. Individuos de *Masius* buscaron comida solitariamente y en grupos multi-específicos, y se alimentaron en 12 especies de plantas de 4 familias. Los machos ocuparon territorios de 30–40 m de diámetro disputados en “leks,” o áreas de despliegues colectivos, dispersos. Los despliegues de cortejo de los machos se ejecutaron sobre troncos caídos y contrafuertes adentro de cada territorio. El repertorio de cortejo incluyó un complejo despliegue de acercamiento al tronco, y despliegues de apuntar la barbilla hacia abajo e inclinarse de lado-a-lado. Parejas de machos ejecutaron despliegues coordinados, pero la función de estos comportamientos es desconocida. Un análisis filogenético de los despliegues de cortejo indica robustamente que *Masius* es el grupo-hermano del género *Corapipo*, y que

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The color frontispiece of a Golden-winged Manakin (*Masius chrysopterus*) male below a female at a buttress root display site is a mixed media painting by Paul K. Donahue.



el género *Ilicura* estaría emparentado más cercamente a éstos. Estas conclusiones sistemáticas están corroboradas en parte, por evidencia morfológica y bioquímica.

Many species of the Neotropical manakins (Pipridae) are known for their extreme sexual dimorphism, elaborate courtship displays, and lek breeding systems (Sick 1959, 1967; Snow 1963a). The patterns of variation in behavior, plumage, and morphology among the 51 species presently classified as manakins (Snow 1979) provide an excellent opportunity to investigate the evolution of nonresource-based, display-polygyny breeding systems, and to study the historical effects of sexual selection on behavioral and morphological diversification. As the courtship displays, breeding systems, and life histories of more manakin species are described, it will become increasingly possible to explore these various evolutionary questions comparatively across the family.

The monotypic genus *Masius* is found in mossy forest of the upper tropical and lower subtropical zones (500–2100 m) of the eastern and western slopes of the Andes from northwestern Venezuela to northern Peru (Meyer de Schauensee 1966, Snow 1979, Hilty and Brown 1986). The behavior of *Masius* is virtually unknown (Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986), and its systematic relationships to other genera of manakins are enigmatic (Snow 1975).

In this paper we present the results of a field investigation of the diet, foraging behavior, and courtship display of the Golden-winged Manakin (*Masius chrysopterus*) in western Ecuador. We also present a phylogenetic analysis of the systematic relationships of *Masius* to other piprid genera based on courtship display behavior.

STUDY AREAS AND FIELD METHODS

Observations were made at two study sites in western Ecuador between 11 May and 28 July 1985. The first site was primary, mossy cloud forest at 1400–1700 m on Hacienda San Vicente, Mindo, Provincia de Pichincha (00°02'S, 78°48'W). The second site was selectively cut and second-growth mossy forest at 500–600 m near the village of El Placer, Provincia de Esmeraldas, on Km 303 of the Quito-San Lorenzo railroad, approximately 24 km WNW of Lita, Provincia de Imbabura (00°52'N, 78°28'W). Both sites were extremely moist; rain was recorded on nearly every day of observation, and direct sunlight was recorded on less than 20 days. Mindo is apparently seasonally drier than El Placer, which experiences much less seasonal change in precipitation (residents of Mindo and El Placer, pers. comm.). The mossy cloud forest at Mindo had an average canopy height of 10–15 m. The forest at El Placer had a canopy height of 20 m and was unusually cool and mossy for its altitude. Apparently, the extremely humid and cool conditions in this portion of the Pacific slope of the Andes and the position of El Placer in the first foothills above the Pacific coast make it possible for mossy forest to persist at much lower altitudes in this region than in other areas of the Andes.

We watched foraging male and female *Masius* for 50 h at Mindo from 11 May to 22 June

1985; none of these individuals was banded, but at least 2 adult males, 2 immature males, and 1 immature male or female were observed. We completed 164 h of observation of territorial males and 2 h of observation of foraging males and females at El Placer from 27 June to 28 July 1985. Seven adult males and one immature male were color banded, weighed, and measured in five days of mist-netting at El Placer from 29 June to 3 July. Vocalizations were recorded with Uher 4000 and Sony TCM 5000 tape recorders. Sonagrams were prepared with a Kay Digital Sonagraph 7800. Color 16-mm movies of the courtship displays were used to prepare the illustrations of the displays. Herbarium specimens of fruit plants eaten by *Masius* were identified and deposited at the University of Michigan Herbarium, Ann Arbor, Michigan.

PLUMAGE AND WEIGHT

Adult male *Masius* are velvety black with patches of bright golden-yellow (Spectrum Yellow, Smithe 1975) on the tail, wing linings, flight feathers, throat, and forecrown, and a patch of orange, red, or brown on the hindcrown (see Frontispiece). Primary and secondary flight feathers and the outer tail feathers are entirely yellow with thin black stripes along the leading edge of their outer vanes. These black edges often conceal the yellow wing and tail patches when the male is perched. The yellow forecrown is composed of thin, plush feathers that curve forward over the culmen and which may be erected posteriorly to produce a slight crest at the top of the head. The posterior half of the crown is composed of orange, red, or brown barbless feathers that are thickened and blunt in shape, and smooth and shiny in texture (similar to specialized feathers of *Bombycilla* and *Chlorochrysa*). The posterior portion of the crown cannot be erected. Laterally bordering the forecrown are two short black plumes that can be erected to form "horns" on either side of the head. Female *Masius* are generally olive-green in plumage with yellow-olive on the throat, belly, and wing linings (see Frontispiece). Immature male *Masius* first resemble females and then molt into adult male plumage. This transition begins with the yellow forecrown and throat patches and then proceeds patchily throughout the rest of the body. Both sexes have dark brown irises, purplish-pink legs, and pinkish-gray bills. Males at El Placer averaged 10.2 g (range = 9.0–12.5; N = 8), and a single female at El Placer weighed 13.5 g.

DIET AND FORAGING BEHAVIOR

Golden-winged Manakins fed on both insects and fruit during short hovering sally flights. Individuals were observed feeding on the fruits of 10 species of plants from four families: Boraginaceae—*Cordia* sp.; Melastomataceae—*Miconia theaezans*, *M. cf. arbicola*, *M. sp.#1* (sect. Cremanion), *M. sp.#2* (sect. Cremanion); Poaceae—*Olyra* sp.; Rubiaceae—*Ossaea* sp., *Palicourea* sp., *Psychotria cf. aviculoides*, *Sabicea* sp. (aff.

umbellata and *colombia*). The most important plants in the diet were the four species of *Miconia*. At Mindo, *Masius* spent almost all of their time foraging at small trees of *Miconia* cf. *theaezans*, which were fruiting abundantly there during the observation period; individuals were observed feeding only once at each of the other three species of food plants collected at Mindo. At El Placer, *Masius* were observed foraging at a wider variety of species of melastomes and Rubiaceae, including *Miconia* cf. *theaezans*.

When foraging, both sexes gave high, thin *tseet* notes (Fig. 1A) at a frequency of once every 1–20 min. These notes are extremely similar to many given by common *Tangara* tanagers at Mindo, but can be differentiated by the high, sharp quality of the initial portion of the descending call.

At Mindo, the male and female *Masius* spent over 75% of 50 h of observation foraging in multispecies flocks. This figure may be exaggerated because foraging *Masius* were most easily detected by the *tseet* notes which were given with increasing frequency during interactions with a multispecies flock. Foraging flocks included 5–10 species at a time of a total of 15 species, 7 of which (*) were nearly constantly present: *Eubucco bourcierii*, *Dendrocincla fuliginosa*, *Lepidocolaptes affinis*, *Phylidor rufus*, *Terenura callionota*, *Myioborus miniatus**, *Euphonia xanthogaster**, *Chlorochrysa phoenicotis*, *Tangara rufigula*, *T. arthus**, *T. icterocephala*, *T. xanthocephala**, *T. parzudakii**, *T. laboradorides**, *T. ruficervix*, *T. gyrola*, *T. nigroviridis**, *T. vassorii*, *Anisognathus flavinucha*, and *Piranga leucoptera*. During the observation period, the multispecies flocks foraged almost exclusively at *Miconia* cf. *theaezans* trees and a few other large melastomes over 6 m high. Multispecies flocks traveled at a rate of 100 m/h or more and had home ranges of at least 300 m in diameter. One to three individual *Masius* were observed in a single foraging flock at a time; a single adult male was nearly always present and immature males-females were the least frequent. Adult male *Masius* often aggressively chased female-plumaged and immature male *Masius*, excluding them from specific feeding perches or trees, and perhaps resulting in their lower frequencies of attendance at flocks. *Masius* sometimes dropped out of these flocks to continue foraging at a particular tree, or to preen. Adult males at Mindo rarely gave advertisement calls (see below), and they did not exhibit any nonresource territoriality indicative of lek behavior.

Although less time was spent observing foraging individuals at El Placer (2 h), it appeared that *Masius* at this locality did not associate with multispecies flocks frequently. In over 10 h of observation of multispecies flocks at El Placer, *Masius* was only occasionally in attendance. More typically, they foraged singly or in groups of two or three at a variety of heights from 2 to 20 m. Territorial males had several small fruit sources within their territories, which they fed on occasionally throughout the

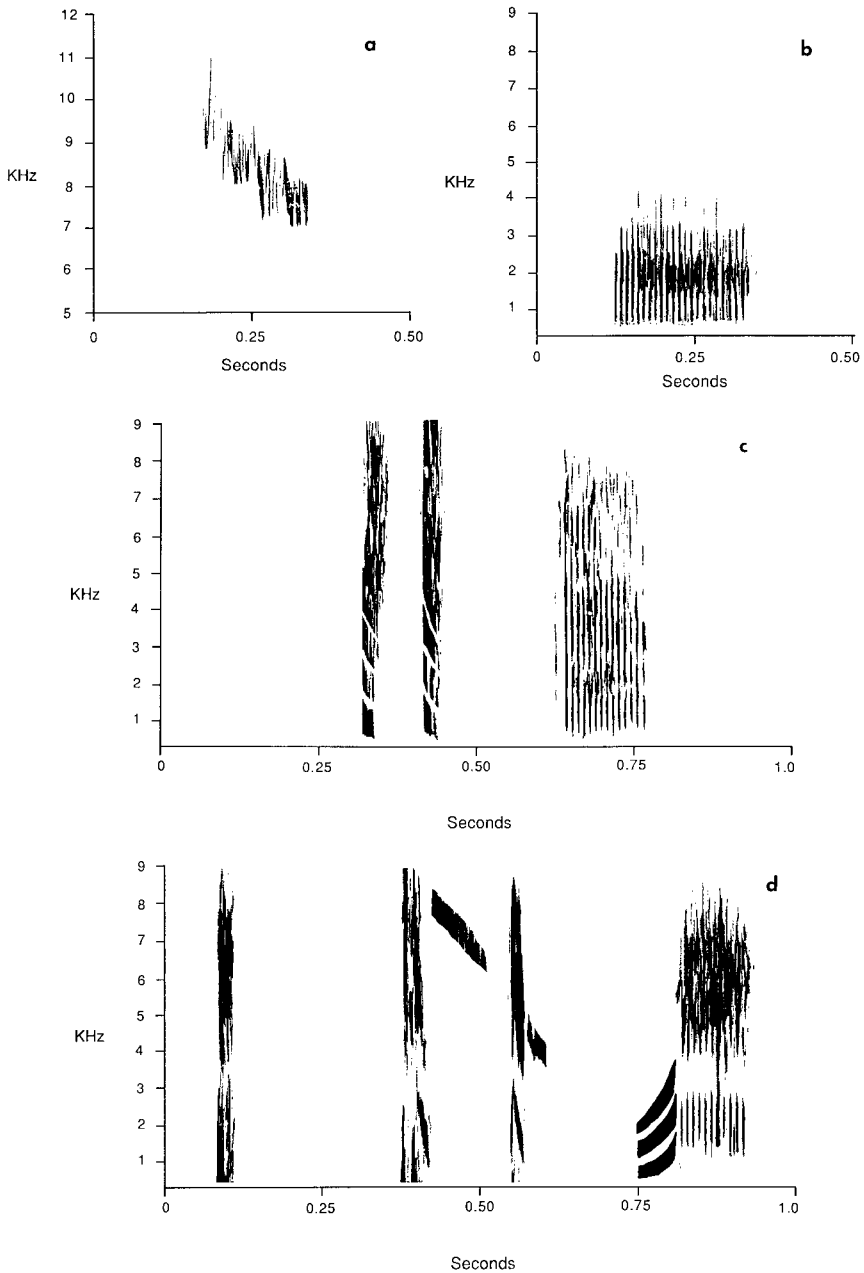


FIG. 1. Sonograms of vocalizations of *Masius chrysopterus*: (A) foraging call, *tseet*; (B) advertisement call, *nurrt*; (C) display call, *tseet-tseet-nurrt*; (D) display call of *Corapipo gutturalis*, *pop-tickee-yeah* (see Prum 1986).

day. At particularly large fruit sources, individual *Masius* were sometimes observed in the same tree with as many as eight other bird species, including the Club-winged Manakin (*Machaeropterus deliciosus*) and the Green Manakin (*Chloropipo holochlora*). These groups, however, rarely traveled among fruiting trees in coherent associations.

SPATIAL DISTRIBUTION OF MALE TERRITORIES AND DISPLAY SITES

Male *Masius* defended territories between 25–40 m in diameter with frequent advertisement calling (see below). At the main observation site, three males maintained adjacent territories that were in auditory range of each other. This group of males was separated by 150 and 300 m, respectively, from the two nearest, other groups, which were each composed of two or more males. The male observed most extensively (W/W) sang over an area of about 25×40 m, but spent over 90% of its calling time within 10 m of the main display log. W/W was in attendance on his territory in over 90% of 5-min observation periods (47 h) over 15 days. In 35 h of observation of two other territorial males (G/G, and unbanded), territorial attendance was much less consistent and averaged less than 50%.

Each male territory included 2–4 fallen-log or exposed buttress-root display sites. Nine display logs and roots were located. They varied from 15 to 100 cm in diameter and 0.5 to 10 m in length and were generally free from obstructing vegetation. W/W displayed at four different logs; two of these logs were 5 m apart and formed the center of his territory, and the two other logs were 10 and 15 m away from the first two. G/G displayed at an exposed buttress root and a log that were 40 m apart at the extreme ends of his calling territory. The closest display logs of W/W and G/G were about 15 m apart.

ELEMENTS OF THE COURTSHIP DISPLAY

Advertisement calling.—The male advertisement call was a low, nasal, frog-like *harrnt* or *nurrt* (Hilty and Brown 1986) (Fig. 1B). Occasionally, the *nurrt* and *tseet* calls were combined into a single, continuous *tseet-nurrt*. Males called from many 2–4 m high perches throughout their territories, sometimes returning habitually to call from specific perches. While calling, males perched with their body plumage fluffed and with heads pulled in, concealing their yellow throat patches. When a male uttered a *nurrt* note, its head popped up briefly exposing the throat patch.

Advertisement calling began in the morning between 07:30 and 08:30 h and continued throughout the day until 18:00 h. The duration and consistency of calling varied greatly among males. In 14 h of continuous

5-min observation periods over 2 days, W/W called at an average rate of 3.2 calls/min. From the time morning activity began until the end of the series of observation periods, W/W called 1579 times in 8 h 10 min (07:50–16:00 h) on the first day, and 1053 calls in 5 h 50 min (07:55–13:45 h) on the second day. There was no consistent variation in calling frequency with the time of day, although hard rains curtailed calling whenever they occurred. The maximum calling frequency recorded in any 5-min observation period was 9.6 calls/min by W/W during a bout of counter singing with neighboring G/G. Other males besides W/W called at similar frequencies when in attendance at their territories, but they did not call as consistently throughout the day.

Log-approach display and display call.—Male *Masius* performed an aerial and vocal display when they approached their fallen-log or buttress-root display sites. For the aerial portion of the display, males flew to the display log from a perch 1–5 m high and 1–10 m from the display log, landed on the display log, immediately rebounded up into the air, and landed 30–40 cm down the log (Fig. 2a). During this rebound, males turned around in flight, exposing their yellow wing patches, which are often obscured in normal flight, and landed facing back in the direction from which they first approached the log. The log-approach display was often given silently ($N = 45$), but in the majority of cases males uttered a highly synchronized display call during the log-approach display ($N = 90$). The display call began as a high, thin, continuous, descending *seee* note which lasted from 1 to 3 sec and was given while in flight from a perch to the display log. Immediately before landing on the log, males gave a double *tseet-tseet* note that was followed immediately by a single, growling *nurrt* during the rebound flight down the log. The entire display call was performed very rapidly producing a continuous *seee . . . ee-tseet-tseet-nurrt* (Fig. 1C). In the sonograms of the display call, the introductory *seee* note appears as a thin band approximately 1 KHz wide which descends from 9 KHz to 7 KHz (not illustrated). The *tseet-tseet* notes are each composed of a number of descending parallel harmonic bands. The final *nurrt* note is composed of a series of 12–18 extremely short notes with harmonics from 0.5–7 KHz which form a single syllable about 0.015 sec long. The display call *nurrt* is very similar to the advertisement *nurrt* in structure (Fig. 1B, C). Log-approach displays were performed throughout the day from 07:30 h until 15:00 h with slightly increased frequency between 08:30 h and 10:00 h. Log-approach displays which were accompanied by display calls were much more commonly observed, but this result could be an artifact of the additional auditory cues for the observers.

Log displays.—The main courtship displays of *Masius* were performed

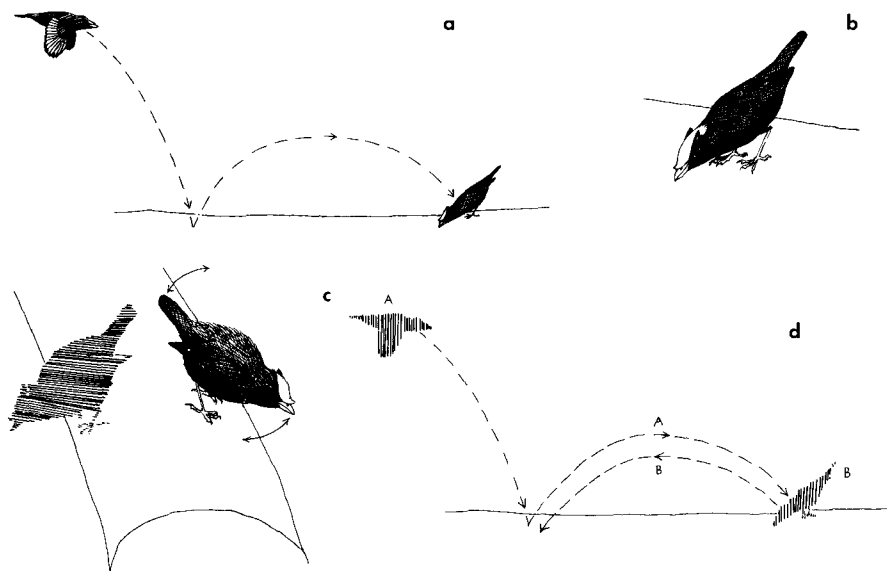


FIG. 2. Displays of *Masius chrysopterus*: (A) Log-approach display and display call. A male flies down to the log, giving a high, thin descending *see* note (left). He then lands on the log and rebounds up, giving the *tseet-tseet-nurrt* portion of the display call (arrows at center). While rebounding off the log, the male turns in flight and lands facing back in the opposite direction (right). (B) The chin-down display. (C) The side-to-side bowing display. A male perches on a display log with his plumage fluffed out, tail cocked, and horns raised, and bows rhythmically from side to side, nearly touching his bill to the log. In between bows, a male (right) may turn 90° to 180° in place or make several short steps before making the next bow (left). (D) Coordinated log-approach display. See text for description.

on mossy fallen logs and exposed buttress roots (see Frontispiece). Once perched on the display log, males performed several distinct display elements.

Chin-down display.—While performing the chin-down display, males remained motionless with their bills nearly touching the log and their tails pointing upward at a steep angle between 60 and 90° (Fig. 2B). The body plumage was sleek in appearance, and the feathers of the yellow forecrown and black horns were erected. Males maintained this posture motionlessly for 1 to 20 sec. The chin-down display was most often performed immediately following log approaches.

Side-to-side bowing display.—Males performed an elaborate “mechanical” display in which the posterior forecrown feathers and “horns” were erected, the body plumage was fluffed out, and the tail held cocked at an angle. In this posture, males bowed rhythmically from left to right, raising

their tails, lowering their heads, and nearly touching their bills to the log (Fig. 2C). Between bows, males either turned 90–180° in place or made a few quick steps in the direction of the next bow. Each successive bow was separated by 0.5 to 1 sec. Males oriented along the long axis of the log, bowing toward either side, or facing one side of the log and bowing toward either end. Males performed this display for 30–60 sec without interruption. The side-to-side bowing display was always performed silently. This display was given during periods of increased calling and display activity, such as following repeated log approaches and display calls, and during intraspecific interactions (see below).

Stamping.—On several occasions males that were perched on display logs stamped their feet very rapidly for <1 sec, moving 2 or 3 cm ahead along the log. Although this display was infrequent and extremely short in duration, it appeared to have the stylized and nonfunctional qualities of a ritualized display behavior and was always performed while perched on the log in between bouts of side-to-side bowing.

Gardening.—While perched on a display log, males often pecked at moss and vegetation on the surface of the log or in the area immediately surrounding the log. “Gardening” behavior does not qualify as a display, but it is included here because it was always performed during bouts of log display.

MALE-MALE INTERACTIONS

Male advertisement calling usually increased in frequency and intensity during counter-singing with a neighboring male, and occasional bouts of aggression on territorial borders were observed. Nonresident adult and immature males sometimes called and displayed in male territories when the resident male was absent ($N = 8$). None of the visitors was banded. Display by visiting males included all the display elements described above, though many of the visiting immature males were obviously less adept at the displays than the adult males.

On about 20 occasions, pairs of males were seen displaying simultaneously on a territory. In two of these instances, the pairs were composed of two visiting males, either two adults or an adult and an immature. In the remaining instances, the pairs were composed of a resident male (G/G) and a visiting, unbanded immature male. Commonly, pairs of males began by counter-singing (*nurrt*s) and then proceeded to perform repeated log approaches and display calls. Once both males were perched on the log, they frequently engaged in synchronized or coordinated side-to-side bowing ($N = 10$). In the coordinated form of the side-to-side bowing display the males faced each other, separated by 10–20 cm, and bowed to either side at the same time. On one occasion, a pair of visiting adult

males performed synchronized side-to-side bowing while perched next to one another about 2 m high and about 4 m from a display log. W/W was never observed displaying with another male.

In five instances, G/G and an unbanded immature male performed a highly coordinated form of the log-approach display (Fig. 2D). While one male (male A) was approaching the log and giving the introductory *see* note of the display call, the second male (male B) was perched on the log. As in a normal log-approach display, male A landed on the log 30–40 cm away from male B and then rebounded up from the log toward male B, giving the full display call. During the rebound, male B hopped along the log underneath male A, turned around in flight, and landed at the place where male A first landed, while male A came to rest at the same point where male B was originally perched. After pausing for a brief moment in this position, male B flew off and the display was repeated 10–30 sec later with the roles reversed. Often at the end of the display before male B flew off, both males perched in chin-down posture, facing each other without moving for a second or two. If male A assumed chin-down posture at the end of his approach, he often remained in that posture until male B began the introductory *see* notes of the next display. At this time male A abandoned the chin-down posture and looked around in anticipation of the arrival of male B. The display occurred extremely rapidly and was always perfectly coordinated. The cycle was repeated between four and 10 times.

MALE-FEMALE INTERACTIONS

As females were impossible to distinguish from some immature males by plumage alone, behavioral criteria were used to identify presumptive females at the display sites. Adult and immature males always displayed or assumed some display posture, such as raising the forecrown and horn feathers, when visiting a display site. On three occasions, female-plumaged birds visited calling perches and display logs on a male territory without calling, attempting to display, or assuming any overtly male posture. In each instance the resident adult male (W/W) performed repeated log-approach displays, display calls, chin-down and side-to-side bowing displays to the presumptive female for between 1 and 5 min. In many of these log approaches, W/W landed first on one side of the perched female and rebounded over her landing on her other side. When the chin-down posture was performed W/W perched directly in front of the female and remained motionless for several seconds. During the side-to-side bowing display, he bowed to the left and to the right of the visiting female, clearly displaying his crown feathers with each bow. Sometimes he moved slowly toward the female with short steps between each bow, eventually dis-

placing her from that place on the log. All three interactions ended with both birds flying off. No copulations were observed. A female mist-netted at El Placer on 28 July had a well developed brood patch, indicating that females were nesting and actively soliciting mates during the time of the observations. The breeding season at Mindo has yet to be determined.

COMPARISONS OF DISPLAYS OF *MASIUS* TO OTHER PIPRIDAE

The courtship displays of *Masius* share striking and unique similarities with those of the genus *Corapipo*. The displays of the Central American subspecies of *Corapipo leucorrhoa* have been described briefly (Aldrich and Bole 1937, Slud 1964, Skutch 1967), but the display behavior of *Corapipo gutturalis* of the Guiana Highlands has been documented in some detail (Prum 1986). Both *Masius* and *Corapipo* perform their courtship displays on fallen logs or buttress roots in a manner which is unique among known manakins. The log-approach displays performed by *Masius* and *Corapipo* are identical in many respects. In both genera, males fly to the display log, immediately rebound off the log and land down the log, facing back toward where they first landed. Both species of *Corapipo* also perform a less rapid "moth-flight" log approach, an elaborate above-the-canopy log approach, and a flight-song display not performed by *Masius*. Both *Masius* and *Corapipo* give stereotyped and highly synchronized display calls during the rapid log-approach display. The display calls of both genera are characterized by (1) a long, thin introductory *see* note or a series of *see* notes which is given while in flight toward the log, (2) a double-syllabled note uttered as the male drops to the log (apparently single-syllabled in *Corapipo leucorrhoa*) (Skutch 1967), and (3) a final, squeaky or harsh, single-syllabled note given as the male rebounds back down the log. Although *Masius* do not produce any mechanical display sounds, both species of *Corapipo* produce a mechanical *pop* note immediately before dropping to the log. Recordings of the display calls of *Corapipo leucorrhoa* are not available, but sonograms of the display calls of *Masius* (*tseet-tseet-nurrt*) and *Corapipo gutturalis* (*pop-tickee-yeah*; Prum 1986) reveal some basic similarities in the structure of the two calls (Fig. 1C, D). The paired *tseet-tseet* and *tickee* notes are very similar in structure, and the final *nurrt* and *yeah* notes are nearly identical in form. (The final portion of the *yeah* note was incorrectly left out of the sonograms of the *Corapipo gutturalis* display call in Prum 1986). *Corapipo gutturalis* also has descending notes following each syllable of the *tickee* notes and a band of ascending harmonics preceding the *yeah* note, both of which are lacking in *Masius*. The *Masius* display call is slightly faster in tempo and lacks the introductory mechanical *pop* note.

The side-to-side bowing and chin-down displays of *Masius*, the wing-

shiver and hunched-posture displays of *Corapipo gutturalis*, and the general log displays of *Corapipo leucorrhoa* all involve a very specific posture in which the bill and foreparts are lowered until nearly touching the display log and the hindparts are distinctly raised. The side-to-side bowing display is unique to *Masius* whereas the wing-shiver and bill-pointing are unique to *Corapipo gutturalis*.

Some of these behavioral similarities are shared by the monotypic Pin-tailed Manakin (*Ilicura militaris*) of southeastern Brazil (Snow and Snow 1985). The chin-down postures of *Ilicura* and *Masius* appear to be virtually identical; indeed, males of both species even sleek their plumage during the display. The chin-down posture is also similar to the position assumed during the log displays of both *Corapipo* species. Although a "tail-up" posture is performed by the *Pipra aureola* species-group (Snow 1963b, Schwartz and Snow 1978, Robbins 1983), this posture differs in that the bird is oriented perpendicular or oblique to a thin (ca 5 mm) perch, with its head sometimes below the level of the perch. The chin-down postures of *Ilicura*, *Masius*, and *Corapipo* are all performed while oriented parallel to a log or large perch so that the head nearly rests on its surface.

Although generalized to-and-fro flights are a conspicuous element in the courtship displays of several known manakin species (Sick 1959, 1967; Snow 1961, 1962a; Skutch 1969; Prum 1985), there are aspects of the double *snap*-jump of *Ilicura* that this genus shares uniquely with *Masius* and *Corapipo*. Among manakins, only these three genera are known to perform a to-and-fro display in which males fly parallel to a display perch or log, turn rapidly around in midflight and land on the same perch facing directly back toward their original position. This behavioral novelty is exhibited in the log-approach displays of both *Corapipo* and *Masius*, the to-and-fro log display of *Corapipo gutturalis* and the double *snap*-jump of *Ilicura*. All of these displays are performed over the backs of females that visit display sites, implying a similarity in behavioral context as well as in the general appearance of the displays. Male *Chiroxiphia* perform a "cart-wheel" display which also entails jumping along a horizontal perch (Snow 1963b, Foster 1981), but this display lacks the abrupt turn-around in flight and the stereotyped form which characterize the displays of the other three genera.

PHYLOGENETIC ANALYSIS OF DISPLAYS OF *MASIUS* AND OTHER PIPRIDAE

Sick (1959, 1967), Snow (1963a, 1975), and others have recognized phylogenetic patterns in the courtship displays of manakins; however, attempts to formulate explicit systematic conclusions from the behavioral

similarities have been limited both by the lack of sufficient behavioral data and the problem of establishing behavioral homologies between piprid genera. Behavioral homology and the use of behavior in systematics have been discussed in detail (e.g., Atz 1970), and behavioral characters, particularly song, have been widely used in avian systematics (e.g., Payne 1986).

In order to use behavioral similarities as systematic characters it is necessary to distinguish shared derived behavioral novelties or synapomorphies, which imply exclusive common ancestry, from primitive similarities or plesiomorphies, which are not phylogenetically informative. Synapomorphies may be identified by comparing the variety of character states found in the monophyletic group in question (the in-group) to those found in its most closely-related sister-group (the out-group); by out-group comparison, those states unique to some portion of the in-group are hypothesized as derived (Eldridge and Cracraft 1980, Stevens 1980, Wiley 1981). A phylogeny may be constructed by hierarchically arranging these derived character states.

The position of *Masius* within the piprids has been enigmatic (Snow 1975). In an investigation of tyrannoid allozymes, S. M. Lanyon (1985) found that a monophyletic group containing the piprid genera *Masius*, *Corapipo*, *Chiroxiphia*, and *Chloropipo* was supported by a variety of distance and cladistic analyses, but that the relationships among these genera could not be consistently resolved. The sister-group to this clade was comprised of *Pipra*, *Manacus*, *Tyrannneutes*, and *Neopelma* (Lanyon 1985). Using the former as an in-group and the latter as an out-group, it is possible to polarize the behavioral similarities described above and produce a behavioral phylogeny of the genera *Masius*, *Corapipo*, and *Chiroxiphia*. The genus *Ilicura* was not included in Lanyon's analysis (1985) but is included in this in-group on the basis of the behavioral characters alone. The genus *Chloropipo* is not included in this analysis because its courtship behaviors have not been described. The behavioral characters used are motor patterns which are part of courtship display and not the social contexts of these behaviors (Table 1).

The results of this analysis strongly indicate that *Corapipo* and *Masius* are sister-groups and further suggest that *Ilicura* is the sister-group to these two genera (Fig. 3). The placement of *Masius* and *Corapipo* as sister-groups is corroborated by striking similarities in their syringeal structure. Ames (1971) found that *Corapipo* was unique among all passerines examined in the structure of both its syringeal musculature and cartilages. He subsequently observed the syrinx of *Masius* and found it to be nearly identical to *Corapipo* (P. L. Ames, pers. comm.). Ames (1971) reported that the syringes of *Chiroxiphia* and *Ilicura* were distinct from the other

TABLE 1
BEHAVIORAL CHARACTERS USED IN PHYLOGENETIC ANALYSIS OF *MASIUS CHRYSOPTERUS*
AND RELATED PIPRIDAE^a

Derived behavioral characters	<i>Chiro- xiphia</i>	<i>Ilicura militaris</i>	<i>Masius chrysop- terus</i>	<i>Corapipo gutturalis</i>	<i>Corapipo leucor- rhoa</i>
1. Cart-wheel display	1	0	0	0	0
2. Rebound from display perch or log with turn-around in flight	0	1	1	1	1
3. Display postures with foreparts lowered to perch or log	0	1	1	1	1
4. Double <i>snap</i> -jump display	0	1	0	0	0
5. Display on fallen logs or buttress roots	0	0	1	1	1
6. Log-approach display with synchronized display call	0	0	1	1	1
7. Side-to-side bowing display	0	0	1	0	0
8. Flight-song display	0	0	0	1	1
9. Butterfly log-approach display	0	0	0	1	1
10. Mechanical <i>pop</i> in log approach display call	0	0	0	1	1
11. Wing-shiver and to-and-fro displays	0	0	0	1	0
12. Throat patch erected into ruff during display	0	0	0	0	1

^a 0 indicates absence and 1 indicates presence of derived character state. All derived character states were absent in the out-group. See text for details. References: Out-group.—Davis 1949; Prum 1985; Robbins 1983; Schwartz and Snow 1978; Skutch 1969; Snow 1961, 1962a, b, 1963a, b. *Chiroxiphia*.—Foster 1977, 1981; Snow 1963c. *Ilicura*.—Snow and Snow 1985. *Corapipo gutturalis*.—Prum 1986. *Corapipo leucorrhoea*.—Aldrich and Bole 1937, Skutch 1967, Slud 1964.

piprids examined, however the variation in syringeal structure in the family is so great that these differences cannot be considered as evidence against a close relationship among these genera. The placement of *Ilicura* in this group should be considered as a preliminary systematic prediction based on behavioral characters that should be tested by further morphological and biochemical investigation.

DISCUSSION

The composition of the diet of *Masius* is similar in many respects to those of some other manakins (Snow 1962a, b; Worthington 1982). As in many other piprids, melastomes of the genus *Miconia* are the most important plant food sources in the diet of *Masius*, followed closely by rubiaceous trees and shrubs. Our observations are too limited to conclude whether the differences in foraging behavior at the two sites were due to

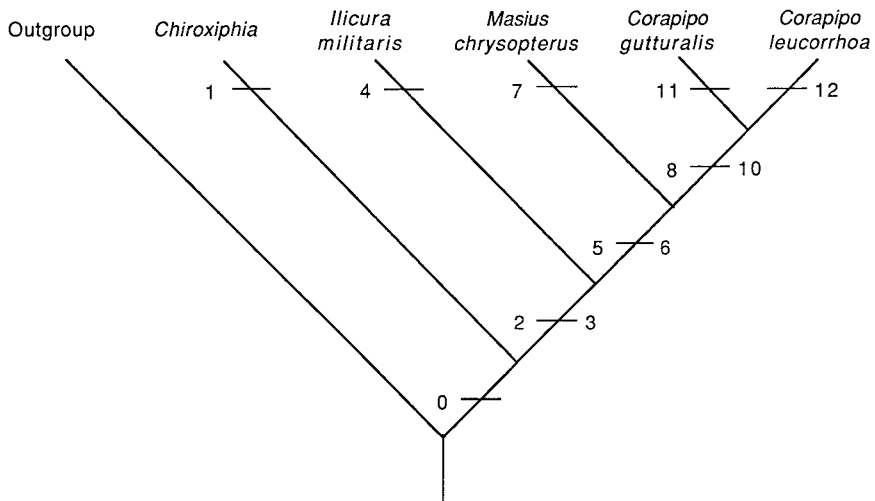


FIG. 3. A phylogeny of *Masius* and related manakins based on derived behavioral characters. Monophyly of the group *Masius*, *Corapipo*, and *Chiroxiphia* is based on (0) derived biochemical characters (Lanyon 1985); biochemical character states of *Ilicura* are unknown. The out-group includes *Pipra*, *Manacus*, *Tyrannneutes*, and *Neopelma* (Lanyon 1985). The polarity and distributions of the behavioral characters (1–12) are detailed in Table 1. See text for description of methods.

seasonal variations in fruit availability or breeding season, or to differences in multispecies flock composition.

Masius appears to maintain display territories in dispersed leks in a manner similar to the *Pipra aureola* species-group (Snow 1963b; Schwartz and Snow 1978; Robbins 1983, 1986), the *Pipra serena* species-group (Skutch 1969, Prum 1985), *Pipra pipra* (Snow 1961), and *Ilicura militaris* (Snow and Snow 1985). Male *Masius* also perform coordinated displays with one another. Unlike Foster (1985), we define coordinated male displays as cooperative only if these behavioral patterns assist in the attraction of mates for one of the males; if a coordinated display does not serve to attract mates (e.g., ritualized aggressive behavior), it does not enhance the fitness of one male through the investment of another, and the behavior cannot be viewed as “cooperative.” Given limited observations, it is not possible to identify the function of coordinated display in *Masius*. The individual variation in frequency of the behavior and the observations of female-visits in the absence of coordinated display indicate that the coordinated behavior of *Masius* is not obligately cooperative as in

Chiroxiphia (Snow 1963c; Foster 1977, 1981), and may not serve in the cooperative attraction of females at all. The male that was most consistently in attendance on his territory and that received all three observed female visits was never observed displaying with another individual. In the composition of intermale partnerships, the coordinated behavior of *Masius* appears to be most similar to the nonobligate cooperative displays of the *Pipra aureola* species-group (Snow 1963b; Schwartz and Snow 1978; Robbins 1983, 1986), but the behavior of *Masius* also appears less frequent and consistent than the coordinated displays of these species. In the *Pipra aureola* species-group, the subordinate male of a partnership has the opportunity of deposing the alpha male or inheriting the alpha male's territory (Robbins 1983, 1986). Further observations are required to determine whether this is a plausible mechanism for the maintenance of coordinated display behavior in *Masius*.

The congruence between the phylogenetic analysis of courtship displays presented above, derived biochemical characters (Lanyon 1985), and morphological evidence from the structure of the syrinx (Ames 1971, pers. comm.) strongly supports the systematic conclusion that *Masius* and *Corapipo* are sister-groups. Confidence in this sister-group relationship permits us to investigate explicitly various aspects of the divergence between the two genera. For instance, certain vocal elements common to both genera have undergone a transference of function; the *Masius* advertisement call is clearly similar to the final note of the display call, whereas *Corapipo*'s advertisement call is an elaboration of the introductory *see* notes of the display call (Prum 1986).

Although many elements of the courtship displays of these two genera have been conserved since common ancestry, their male plumages have diverged considerably. The conservation of these behavioral traits could be due to fixation of genetic factors determining behavior. Alternatively, the difference in the rate of divergence of behavioral and morphological traits may suggest that females in this lineage have been choosing mates on the basis of variation in morphological plumage traits rather than behavioral characteristics. If female mate preferences are acting on variation in heritable male traits, then these male traits should evolve faster than others (Fisher 1958; Lande 1980, 1981; Payne 1983; West-Eberhard 1983). The divergence in male plumage could also be the result of natural selection for premating isolation mechanisms. Such selection would result in reproductive character displacement which is restricted to or accentuated in zones of sympatry, while sexual selection would produce differentiation without any geographical correlation (Payne 1983). *Masius* and *Corapipo* are sympatric in parts of all three ranges of the Colombian Andes (Hilty and Brown 1986), but male character divergence is neither

restricted to nor accentuated in these zones of contact. Thus, the hypothesis that sexual selection has produced male plumage divergence in this group is corroborated, though the mechanism for the conservation of courtship behaviors remains to be elucidated.

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LITERATURE CITED

- ALDRICH, J. W. AND B. P. BOLE. 1937. The birds and mammals of the Azuero Peninsula (Republic of Panama). Sci. Publ. Cleveland Mus. Nat. Hist. 7.
- AMES, P. L. 1971. The morphology of the syrinx in passerine birds. Peabody Mus. Nat. Hist. Bull. 37.
- ATZ, J. W. 1970. The application of the idea of homology to behavior. Pp. 53-74 in Development and the evolution of behavior (S. Coopersmith, ed.). Freeman, San Francisco, California.
- DAVIS, T. A. W. 1949. Field notes on the Orange-crested Manakin *Neopelma chrysocephalum* (Pelz.). Ibis 91:349-350.
- ELDRIDGE, N. AND C. CRACRAFT. 1980. Phylogenetic systematics and evolutionary process. Columbia Univ. Press, New York, New York.
- FISHER, R. A. 1958. The genetical theory of natural selection. Dover, New York, New York.
- FOSTER, M. S. 1977. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. Am. Nat. 111:845-853.
- . 1981. Cooperative behavior and social organization of the Swallow-tailed Manakin (*Chiroxiphia pareola*). Behav. Ecol. Sociobiol. 9:167-177.
- . 1985. Pre-nesting cooperation in birds: another form of helping behavior. Pp. 817-828 in Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds.). Ornithol. Monogr. 36.

- HILTY, S. L. AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 36:213–223.
- . 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Nat. Acad. Sci.* 78:3721–3725.
- LANYON, S. M. 1985. Molecular perspectives on the higher-level relationships in the Tyrannoidea (Aves). *Syst. Zool.* 34:404–418.
- MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Livingston Press, Narberth, Pennsylvania.
- AND W. H. PHELPS, JR. 1978. A guide to the birds of Venezuela. Princeton Univ. Press, Princeton, New Jersey.
- PAYNE, R. B. 1983. Bird songs, sexual selection and female mating strategies. Pp. 50–90 in *Social behavior of female vertebrates* (S. K. Wasserman, ed.). Academic Press, New York, New York.
- . 1986. Bird song in avian systematics. *Current Ornithology* 3:87–126.
- PRUM, R. O. 1985. Observations of the White-fronted Manakin (*Pipra serena*) in Suriname. *Auk* 102:384–387.
- . 1986. The displays of the White-throated Manakin *Corapipo gutturalis* in Suriname. *Ibis* 128:98–102.
- ROBBINS, M. B. 1983. The display repertoire of the Band-tailed Manakin (*Pipra fasciicauda*). *Wilson Bull.* 95:321–342.
- . 1986. Social organization of the Band-tailed Manakin (*Pipra fasciicauda*). *Condor* 87:449–456.
- SCHWARTZ, P. AND D. W. SNOW. 1978. Displays of the Wire-tailed Manakin. *Living Bird* 17:51–78.
- SICK, H. 1959. Die Balz der Schmuckvögel (Pipridae). *J. Ornithol.* 100:269–302.
- . 1967. Courtship behavior in manakins (Pipridae): a review. *Living Bird* 6:5–22.
- SKUTCH, A. F. 1967. The life histories of Central American highland birds. *Publ. Nuttall Club* 7.
- . 1969. Life histories of Central American birds. III. Pacific Coast Avifauna 35.
- SLUD, P. 1964. The birds of Costa Rica: distribution and ecology. *Bull. Am. Mus. Nat. Hist.* 128.
- SMITHE, F. B. 1975. Naturalist's color guide. Am. Mus. Nat. Hist., New York, New York.
- SNOW, B. K. AND D. W. SNOW. 1985. The display and related behavior of the Pin-tailed Manakin. *Wilson Bull.* 97:273–282.
- SNOW, D. W. 1961. The displays of the manakins *Pipra pipra* and *Tyranneutes virescens*. *Ibis* 103:110–113.
- . 1962a. A field study of the Black-and-White Manakin, in Trinidad, West Indies. *Zoologica* 47:65–104.
- . 1962b. A field study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad. *Zoologica* 47:183–198.
- . 1963a. The evolution of manakin courtship displays. *Proc. Int. Ornithol. Congr.* 12:553–561.
- . 1963b. Displays of the Orange-headed Manakin. *Condor* 65:44–48.
- . 1963c. The display of the Blue-backed Manakin, *Chiroxiphia pareola*, in Tobago, W. I. *Zoologica* 48:167–176.
- . 1975. The classification of the manakins. *Bull. Br. Ornithol. Club* 95:20–27.
- . 1979. Pipridae. Pp. 245–280 in *Check-list of birds of the world*. Vol. 8 (M. A. Traylor, ed.). Museum of Comparative Zoology, Cambridge, Massachusetts.

- STEVENS, P. F. 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.* 11: 333–358.
- WEST-EBERHARD, M. J. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* 52:155–183.
- WILEY, E. O. 1981. *Phylogenetics*. Wiley and Sons, New York, New York.
- WORTHINGTON, A. 1982. Population sizes and breeding rhythms of two species of manakins in relation to food supply. Pp. 213–225 *in* *The ecology of a tropical forest* (E. M. Leigh, A. S. Rand, and D. M. Windsor, eds.). Smithsonian Inst. Press, Washington, D.C.

COLOR PLATE

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