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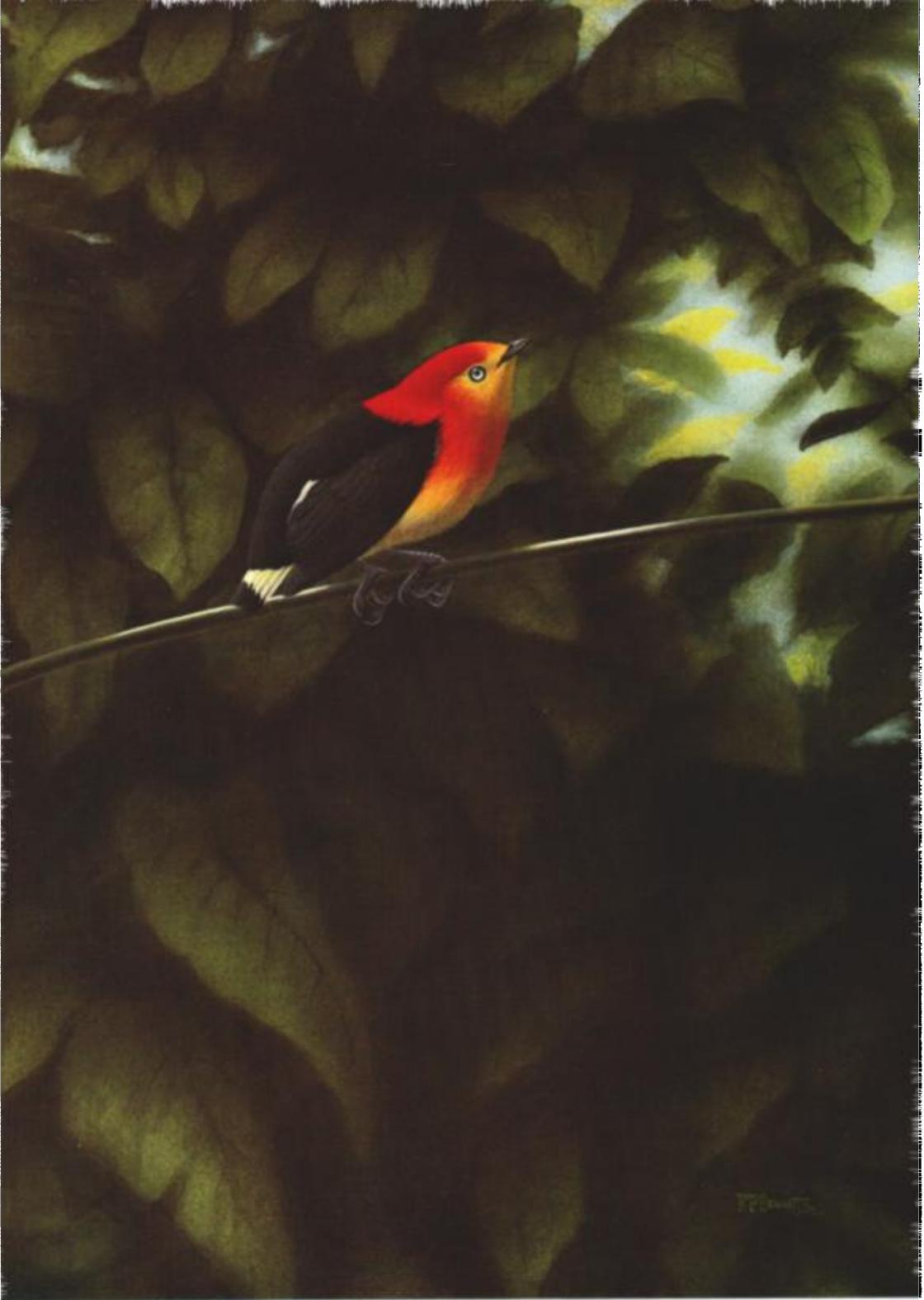
THE DISPLAY REPERTOIRE OF THE BAND-TAILED MANAKIN (*PIPRA FASCIICAUDA*)

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The diversity of mating systems in Neotropical birds is impressive. One family, the manakins (Pipridae), is particularly rich in mating systems; nearly the full gamut is represented among its 51 species (Snow 1979), with most species being promiscuous (Snow 1963b, Sick, 1967). This promiscuity, with its congregations of brightly colored males at leks, is considered to represent the most highly derived type of mating system (Lack 1968). Presumably, a gradual shift in diet from insectivory to frugivory, emancipating males from nesting duties (Snow 1963b), coupled with the nondefensibility of either resources or female groups may have pre-adapted manakins for evolving a lek mating system (Emlen and Oring 1977, Bradbury 1981). Recently, Bradbury (1981) suggested that the crucial selective force in developing lek behavior (given the above conditions) is an increase in female home-range size relative to the size of existing male territories. This may lead to a shift in male strategies from resource defense to self-advertisement and with female preference for clustered males will lead to congregations of displaying males at localized sites within a habitat (Bradbury 1981).

Although something is known about the courtship behavior of nearly half of the manakins (Snow 1963b, Sick 1967), many have yet to be studied. Due to apparent rapid evolution in this group (Schwartz and Snow 1978), different populations of a species may exhibit unique morphological and behavioral characteristics that make it necessary to study each species under a variety of conditions within its range (Sick 1967).

Although the Band-tailed Manakin (*Pipra fasciicauda*) is relatively widespread throughout southern Amazonia (Snow 1979), little information exists about its natural history (Sick 1967, Schwartz and Snow 1978). On the basis of morphology and zoogeography, the band-tail is closely related to



Adult male Band-tailed Manakin, *Pipra f. fasciicauda*
from an acrylic painting by F.P. Bennett, Jr.

the Wire-tailed (*Pipra filicauda*) and the Crimson-hooded (*P. aureola*) manakins; these three species are thought to comprise a superspecies (Haffer 1970). The purpose of my study was to elucidate the display repertoire of *P. fasciicauda* and to compare its behavior with that of the other members of the superspecies complex.

STUDY AREA AND METHODS

The study was carried out in the Tambopata Natural Wildlife Reserve, near the mouth of the Rio La Torre (=Rio D'Orbigny) on the south bank of the Rio Tambopata in the Department of Madre de Dios, Peru (12°50–55'S, 69°17'W) between early June and mid-December 1980. The study site is situated in undisturbed lowland rain forest at about 260 m elevation. The mean annual rainfall is estimated to be 1500–2000 mm and the mean annual bio-temperature to be between 18°C and 24°C (Hartshorn 1979). Puerto Maldonado, ca. 25 km NNE of the study site, averages 1897 mm of rain annually (Oficina Nacional de Evaluación de Recursos Naturales 1976). Relatively little rain fell on the study area from June to mid-September 1980. Rain and strong winds accompanied cold fronts, locally known as "frijajes," from the south every 6–10 days throughout the above period. With the arrival of these cold fronts, temperatures often dropped from about 27°C to near 10°C in just a few hours. By late September storm systems were mainly from the NNE. Rainfall gradually increased through the remaining 3 months of the study.

All five leks visited were in seasonally flooded forest. Apparently, *P. fasciicauda* is restricted to this type of forest (J. V. Remsen and T. A. Parker, unpubl.). The study was concentrated at a single lek that has persisted since at least 1977 (T. A. Parker, pers. comm.). The lek area is transected by several meandering streams that fill at the height of the rainy season (January–mid-March). A stream channel that empties into the Tambopata River dissects the northern end of the area. This stream is completely dry from May–September, with small pools persisting during the early wet and dry seasons. The strong winds associated with the friajes often felled many trees and innumerable limbs. The felling of trees combined with the scant vegetation in the canals created large light gaps in the study area. As a result, the undergrowth (0–5 m) was dense, consisting primarily of melostomes (*Miconia* spp.; Melostomaceae), small palms (Palmaceae), and a number of epiphytic vines (Araceae). Small stands of bamboo (*Guadua* spp.) were scattered throughout the area. Palms were a common and conspicuous element of the middle and upper stories. The broken canopy was generally 20–25 m high with a few emergents reaching 35 m.

The primary observation lek was comprised of 10 territories (Fig. 1). This particular lek was monitored almost daily from ground level blinds 10–25 m from the main display perches. Initially, observations were concentrated at the seven clustered territories; however, one of them was destroyed by a felled tree in late August.

The boundaries (length by width) of each territory were determined by mapping territorial conflicts and the daily movements of the resident male throughout the study. Height of the main perches were rounded to the nearest 0.5 m (Table 1). Dimensions of the display areas were rounded to the nearest 1.0 m. The "main perch to main perch" measurement is the distance from the main perch in a particular territory to the main perch of the nearest territory. In territory 3 (hereafter T3) the main perch used from September through the termination of the study was measured. The main perches of T6 were destroyed before they could be measured. During the initial 3 weeks of the study, approximately 50 individuals (including all territorial owners) were mist-netted and banded with unique color combinations (celluloid leg bands).

Recordings were made with a Uher 4000 Report L tape recorder and Dan Gibson electronic

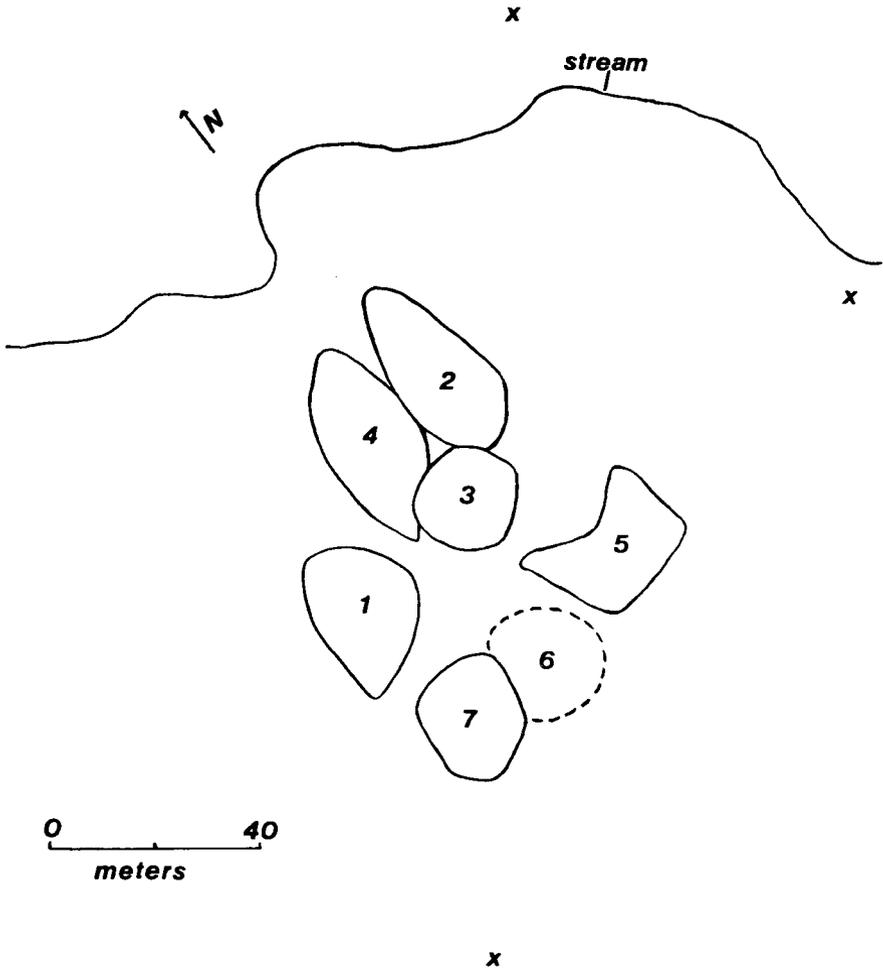


FIG. 1. *P. fasciicauda* lek. Study was concentrated at the six territories indicated by the unbroken lines. The owner of territory 6 (dashed line) abandoned it in August after a felled tree destroyed the main perches. Distances from the stream and the three peripheral territories (indicated by X's) to the clustered territories were estimated.

parabolic microphone (model P500) and were analyzed with a Kay Sonograph Spectrum Analyzer 6061B. Due to the high level of insect noise during many of the recordings, it was necessary to make tracings from the original spectrograms. All spectrograms were made at normal speed and with a wide-band pass filter.

TABLE 1
DIMENSIONS (M) OF SIX *PIPRA FASCIICAUDA* TERRITORIES

	Height of main perch	Size of display area	Intermale distance ^a
T1	4.5	20 × 30	29 (T3)
T2	4.0	18 × 40	14 (T4 & T3)
T3	3.0	20 × 20	14 (T2)
T4	4.5	18 × 45	14 (T2)
T5	5.0	30 × 32	37 (T3)
T7	5.0	20 × 25	45 (T1)

^a Distance of main perch to nearest neighbor's main perch.

DIMENSIONS OF THE DISPLAY AREA

The various parameters of the territories studied are given in Table 1. Most main perches were nearly horizontal or only slightly inclined. Diameter of main perches varied from ca. 10 mm (T4)—ca. 20 mm (T3). With the exception of T3, height of the main perch was similar between territories. Territory 3, the most centrally located, had the smallest display area.

AGE AND SEX DIFFERENCES IN COLORATION

As in most lekking species of manakins, *P. fasciicauda* shows strong sexual dimorphism in plumage. The colorful adult males are clad with striking red, orange, yellow, white, and black feathers (see Frontispiece). The irides are always white. Snow (1962a, b) showed that immature males of White-bearded (*Manacus manacus*) and Golden-headed (*P. erythrocephala*) manakins acquire adult plumage at the beginning of their second year of life, and Foster (1977, 1981) determined that male Swallow-tailed Manakins (*Chiroxiphia caudata*) do not obtain adult dress until the second or third year, while male Long-tailed Manakins (*C. linearis*) require from 2–4 years. In *P. fasciicauda* first-year males seem indistinguishable morphologically from females. The upper parts of immature males and females are uniform olive-green. The breast is yellowish olive-green with the belly and undertail coverts a washed-out yellow. It appears that immature males acquire some adult plumage characters (various amounts of red, yellow, and black) after the first post-juvenile molt. Many females exhibit varying degrees of male plumage characters (Graves 1981). The irides of young males and females vary from brown to gray. Immature males gradually acquire the all white iris. However, irides of adult (skull pneumatized)

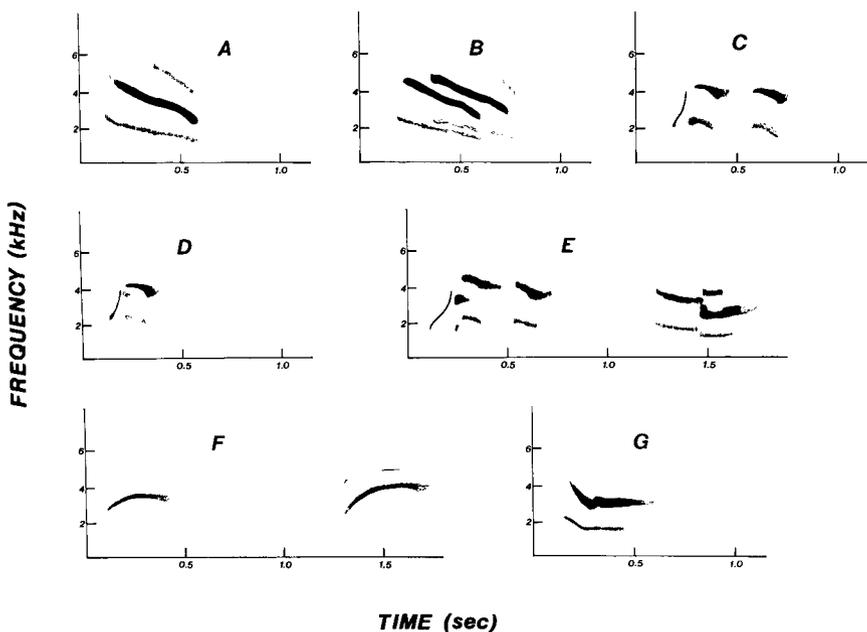


FIG. 2. Tracings of sound spectrograms of vocalizations of *P. fasciicauda*. All tracings were made from original spectrograms and represent the typical pattern of each vocalization. Shown above are the advertisement call (A), two adult males giving the advertisement call in unison (simultaneous call) (B), the "normal" (C), partial (D), and the slurred (E) display calls, two examples of the appeasement whistle given in sequence by the same individual (F), and the culminating call (G). (See text for explanation and function of each vocalization.)

females vary from gray to magenta to white. The legs of all birds are pinkish-purple.

Female-plumaged birds that neither called nor displayed during prolonged visits were assumed to be females. All birds that exhibited some display were considered to be males.

SUMMARY OF SOCIAL ORGANIZATION

A typical Band-tailed Manakin lek consists of several males that maintain closely packed territories. Associated with each court or territory within the lek is an alpha, usually a beta, and occasionally one or more nonterritorial (visitors) adult males that perform coordinated displays to attract and excite females. Alpha males are extremely sedentary and dominate all interactions within their respective territories. Beta males are less sedentary and may display with more than one alpha male per day. Beta

males inherit ownership of territories. Nonterritorial males usually display only briefly at any particular territory and are subordinate to both alpha and beta males. Once a female arrives at a territory, it is only the alpha male that actively courts her. A detailed account of the social organization will be presented in another paper (Robbins, unpubl.).

VOCALIZATIONS AND DISPLAYS

To facilitate comparisons, I have adopted the terminology of Schwartz and Snow (1978) to describe the calls and displays of *Pipra fasciicauda* that are clearly homologous with those of *P. filicauda*.

Vocalizations

“Advertisement call.”—This is the most frequently heard call at *P. fasciicauda* leks. It is the homologue of the “call” of *P. filicauda* described by Schwartz and Snow (1978). This vocalization, *eeew*, is downwardly inflected, from about 5.0–2.5 kHz, and is about 0.5 sec long (Fig. 2A). This call is fairly loud and can be heard more than 100 m away. The caller is always perched; the bill is usually closed and raised 45–60°. The throat is slightly puffed, and the tail is spread, exposing the yellow-white tail band.

While this call undoubtedly advertises a male’s location, this function is likely of limited significance since most adults are probably familiar with the location of the lek. The primary function appears to be to signal that an individual is on his court. A territorial owner invariably calls whenever another manakin passes through his display area. Often the owner gives the call immediately after moving from one perch to another.

An adult male visitor usually gives the call upon entering a resident male’s territory. Frequently an owner and a visiting adult will give the call almost simultaneously (Fig. 2B). Either bird may initiate the call. If the birds are in close proximity, they will raise their bills in unison and call.

“Appeasement whistle.”—This vocalization is a soft, whistled, single note *sweee*, gradually inflected upward from about 2.3 to 4.4 kHz (Fig. 2F). Almost invariably (one exception), the caller is motionless in a normal perched position. The bill may be slightly opened when the call is delivered. Duration is variable, about 0.4 to 0.6 sec or longer, with the same individual occasionally intermingling short and long whistles.

This whistle appears to convey a passive or nonaggressive state of the caller. Commonly, the alpha male, often with feathers puffed out, gives this call early in the morning before display is initiated. Presumably, this signals that a bird is not motivated to display. Likewise, at other times the whistle is given by a visiting bird, apparently to signal that it is not inclined to display with the alpha male. The visiting bird will continue

giving the whistle even after the territorial owner has failed to entice it to the main perch with displays. In addition, the vocalization seems to be used to indicate that the caller is not aggressively inclined. For instance, after a chase sequence one or more of the participants will sit on different perches and give the call.

"Display call."—This abrupt call seems to be given to encourage a bird to display. It is given only from a perched position. The bill is pointed upward about 25–45° and is slightly opened, and the throat is slightly puffed as the vocalization is delivered. The tail is closed. There are three well-defined variations of this call. The "normal" type is composed of three elements, a somewhat harsh *we-ee-eeh* (Fig. 2C). It is given by the alpha male when a visiting bird delays in coming to the main perch to display. Once a display bout has begun, the alpha male virtually never gives the display call. However, a visiting adult male may give this call in the interval between the time the alpha male leaves the main perch and his return with a "swoop-in flight." BA beta male of T1, gave this call about 35% (N = 394 flights) of the time during swoop-in flights by the alpha male. When exchanges between the alpha and beta males are rapid and smoothly coordinated, the vocalization is given less frequently. For example, it was given by the beta male (BG of T5) on only 3 of 23 swoop-in flights performed by the alpha male (RW) during one rapid and well-coordinated display bout (40 swoop-in flights in 14 min). After a break in display, while both birds are resting, the alpha male may give the display call to initiate another round of display.

One distinct variation, referred to as the "partial display call," consists of only the first part of the "normal" call, a *weee*, about 0.25 sec long (Fig. 2D). It is given by an alpha male when a visiting bird (adult male- or female-plumaged) fails to join in display. On these occasions, the owner will fly to the same perch or one adjacent to the uncooperative bird and give the call until the visitor either joins him in display or leaves the territory. In one extreme case, the alpha male, BKR of T2, gave more than 25 of these calls before the visitor left the display area. This version may also be given by either bird of a displaying duet, while on the main perch, when the returning partner (during a swoop-in flight) flies over the perch instead of landing on it. In addition, this call is given more often when two or more males are competing for dominance (particularly during July and August in T2 and T3). A perched male may give the "normal" display call while two or more birds chase each other around the display area. If the chasing continues without any bird joining him in display, he often gives the partial display call. If the chase still continues, he may pursue one or more of the other males.

The third pattern, referred to as the "slurred display call," has an ad-

ditional note that follows about 0.5 sec after the normal version (Fig. 2E). The fourth note is lower in frequency and nearly as long in duration as the "normal" pattern. This call is usually given by the territorial owner when no other birds are present in the display area. This is particularly true in the early morning before any other bird has arrived and late in the afternoon when most display has subsided. The function of this call appears to be the same as that of the above two versions, i.e., to attract other birds to display. The addition of another note of lower frequency probably enhances the transmission of this call over greater distances. Morton (1975) and Marten et al. (1977) have demonstrated that rain forest sounds of lower frequency carry farther than sounds delivered from the same height at a higher frequency.

"*Culminating call.*"—This vocalization (Fig. 2G), a prolonged *eeooo*, is given only during a swoop-in flight. A male performing the swoop-in flight delivers the call the instant before he reaches the main perch. It is rarely omitted during solo performances or between well-acquainted male partners. Between displaying twosomes, the call is usually omitted only when the passive bird fails to bend forward and fly to an adjacent limb as the active male swoops up to the perch. In these instances, the active bird may either land quietly next to the passive bird or will swoop over his head to an auxiliary perch. Immature males rarely give the call. This vocalization may serve in accenting the termination of a swoop-in flight.

"*Klok.*"—This low intensity call is apparently mechanically produced (probably by the wings). Schwartz and Snow's (1978) phonetic representation (*klok*) of the homolog of this call in *P. filicauda*, accurately describes the sound produced by *P. fasciicauda*. The *klok* (Fig. 3A) consists of two pulses of sound about 0.005 sec apart. It is produced primarily in the instant before or upon landing on a perch. Likewise, during a swoop-in flight, a *klok* is produced as a male lands at the distant perch before he returns to the main perch. This sound appears to accent the arrival of a male at a perch.

"*Kloop.*"—Like the shorter *klok*, this low frequency call is apparently produced by the wings (Fig. 3B). It is produced at the lowest point of a swoop-in flight the instant before the male quickly ascends to the main perch. As with the *klok*, the *kloop* probably increases the conspicuousness of the male to other birds. The *kloop* and the culminating call indicate that a swoop-in flight has just been performed.

DISPLAYS

"*Side-to-side display.*"—An individual performing this display is oriented perpendicular to the perch. The body is held rigid, slightly tilted upward, while the head is raised about 45–70°. The crown and upper

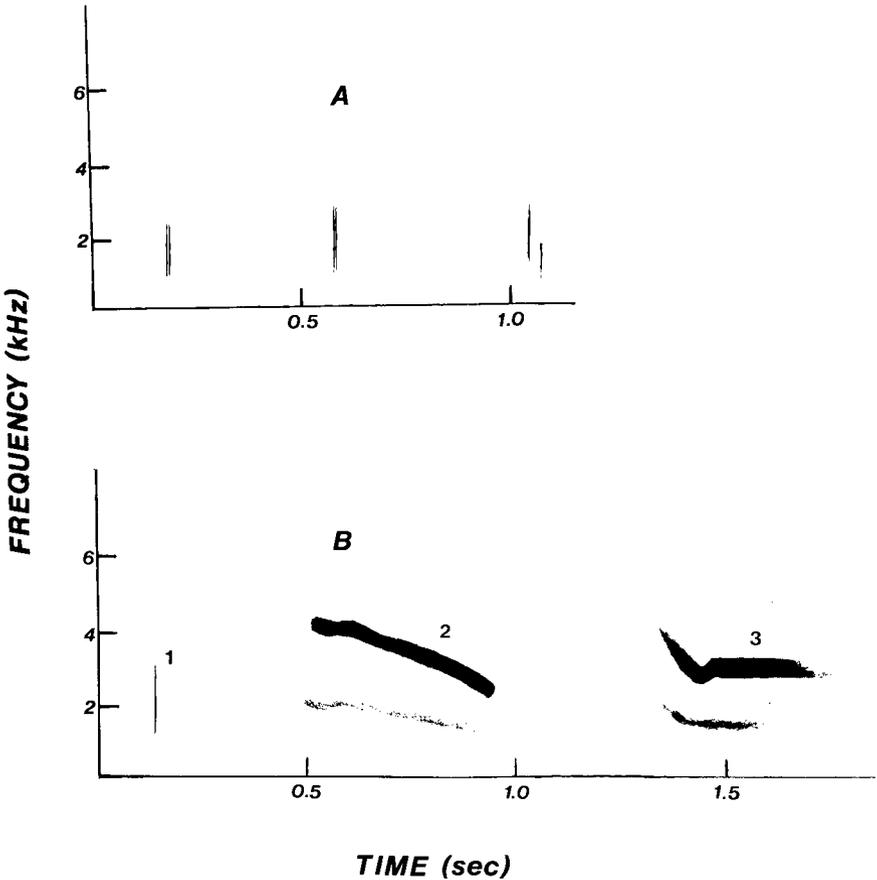


FIG. 3. Tracings of sound spectrograms of calls of *P. fasciicauda*. Three examples of the *klok* are represented (A). (B) Calls given during a swoop-in flight: the *kloop* (1) and the culminating call (3) are given by the active bird during most swoop-in flights; the advertisement call (2) is occasionally given by the passive bird the instant before or as the active bird arrives at the perch. (See text for further explanation.)

mantle feathers are depressed. Normally the bird performs several rapid, short (1–2 cm) hops to one side then back to the original position. The displaying bird usually hops no more than 10 cm in either direction. During this display the bird has a preferred direction that he faces. For example, the direction of orientation was nonrandom for all four alpha males analyzed (Fig. 4). Rarely (<4%, N = 339 observations), a bird may perform

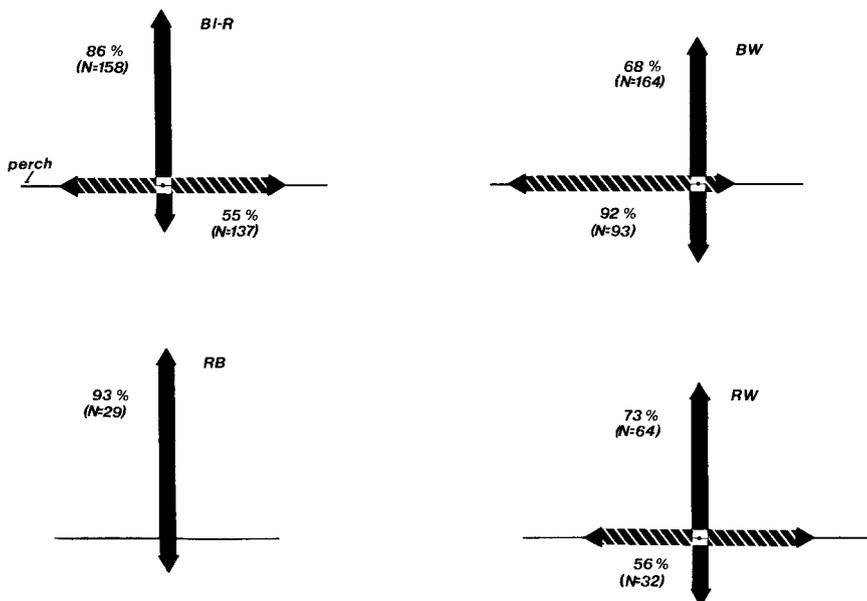


FIG. 4. Degree of asymmetry of two different orientations of the side-to-side display. Solid arrows exhibit the degree of asymmetry (in %) of the direction an alpha male faces while performing the display. This orientation was nonrandom for all alpha males (binomial test, $P < 0.05$, Conover 1971). Cross hatched arrows represent (in %) the degree of asymmetry in the subsequent direction of hopping. Only alpha male, BW, hopped in a nonrandom direction ($P < 0.05$). Data were too few to analyze the degree of asymmetry in the direction of hops of RB.

in one direction, stop, turn around, and display facing in the opposite direction. An owner may have a preferred direction, right or left, to which he hops during each series, although some individuals exhibit no preference, e.g., two of the three alpha males analyzed hopped randomly (Fig. 4). On rare occasions ($<3\%$, $N = 494$ observations), when a bird is especially excited, it may hop in one direction, return to the original position, and then hop in the opposite direction. I do not know whether preferences are reflections of innate "right-or-left-handedness" or of orientation toward some unknown feature of the display site environment.

The territorial owner is the principal performer of this display, e.g., B1-R 97% ($N = 207$), BW 95% ($N = 168$), RB 93% ($N = 29$), and RW 75% ($N = 142$), although a beta male and/or a nonterritorial male will occasionally perform the display. Most displays are conducted on the main

perch, e.g., B1-R 86% (N = 207), BW 90% (N = 168), RB 100% (N = 29), and RW 68% (N = 142). Displays not performed on the main perch are invariably performed on nearby auxilliary perches. The side-to-side display invites a visiting bird to join the performer on the main perch. Its duration is dependent on the response of the visiting bird. If a visitor immediately moves to the main perch, the performer may terminate the display after a single series of hops. However, if the visitor delays, the displayer may perform several series. On two occasions, B1-R (alpha male of T1) performed this behavior for over 2 min with only a few brief (1–4 sec) pauses.

“*Short flight.*”—This is a common element of the display repertoire of *P. fasciicauda*. It may precede or follow any other display. A resident male usually performs this display immediately upon detecting the arrival of another bird in the display area. He usually flies with a normal flight pattern from one perch to another, in a more or less horizontal plane, and the instant before or upon landing produces a *klok*. Not uncommonly, the resident male performs several of these in rapid succession between two perches, primarily the main perch and an adjacent perch. This not only enhances the conspicuousness of the male, but may aid in drawing the visitor’s attention to the main perch.

“*Stationary display.*”—The head is tilted forward, and the body is held nearly horizontal, while the wings are lowered slightly and quivered. The crown and nape feathers are depressed. The lower back feathers may be slightly erected. This behavior may precede or follow any other display and may be performed on any display perch. This display is exhibited when a male is anticipating the actions of another bird. This display was most frequently given when three or more birds were present in a territory. Often one of the birds, observing from a perch, would exhibit stationary displays when two other birds were chasing one another around the display area.

“*Horizontal freeze.*”—The posture of a male performing this display is reminiscent of the stationary display except in the freeze the body, wings, and tail are held in a rigid horizontal position, with the crown and upper mantle feathers depressed. The pupils are contracted. Unlike the stationary display, however, this display is only exhibited in the presence of a female-plumaged bird. On four occasions this behavior was observed without any apparent female-plumaged birds present; however, the male may have detected a female I did not notice. A swoop-in flight followed by a short flight to an adjacent perch immediately precedes the majority of the freezes. This may be one of the ways males assess the receptiveness of females during the course of courtship. Movement by a female during the display appears to initiate an immediate response by the male. For ex-



FIG. 5. Adult male performing the butterfly display.

ample, if the female returns to the main perch the male immediately terminates the freeze and will initiate another form of display. The duration of this display appears to be dependent on the female's actions. Males may remain in this frozen posture up to 10 sec, although the freeze usually lasts no more than 5 sec.

"Butterfly display."—This conspicuous display is performed by an adult male that flies in a more or less direct horizontal plane between display perches (Fig. 5). The flight is deliberate with shallow wing beats. The wings appear to be held fairly stiff and are extended to maximally exhibit the white of the primaries and secondaries. No calls are given during the display, although occasionally a bird will produce a *klok* upon landing. It

may precede or follow any other display and is never performed in the absence of another bird.

"Aerial chase."—This rarely-occurring display ($N = 20$) was observed only during July and August in territories 2 and 3. The display is similar to the butterfly display: participants fly with slow, shallow wing beats conspicuously displaying the white areas of the flight feathers. In contrast to the butterfly display, two birds are always involved, with one chasing the other around in a series of wide loops through and above the display area. The rate of flight is more rapid than a butterfly display. Some of these chases lasted over a minute without either bird landing; one chase lasted about 3.5 min with a 20-sec pause when both birds rested on perches. In all cases, the aerial chase was observed in the presence of three or more adult-plumaged males in the display area. At least three chases terminated in flights. In territory 3, every instance ($N = 7$) involved a visitor, BY or RG, chasing another visitor, BB. The alpha male BWB never participated. Unfortunately, the identity of both participants was not determined in most chases in T2. This display may be one of the means by which a visiting male establishes dominance over other visiting males. Only once was a vocalization heard during the display; in this single instance, one of the participants gave a quivering appeasement whistle.

"Flutter."—This is the copulatory position of a male. The male appears to be falling backward off a perch, with wings spread and rapidly beating, while the head and upper body are slightly tilted forward. At times a male may perform the flutter while raised on his toes. Most instances of this behavior were not during actual copulation but during pseudo-copulations with branches. In these instances, a male flies to a perch and performs the flutter, making contact between the cloacal region and the perch. Most of these pseudo-copulations lasted no more than 4 sec. In 50% of the cases ($N = 110$), the flutter followed a swoop-in flight. On six occasions immature males were observed performing this act. Whether this is an innate response to rising hormone levels or an imitation of other performing males is not clear.

"Tail-up freeze."—Once a male has attracted another bird, male or female, to his display perch, he may perform a tail-up freeze (Fig. 6). The male orients the cloacal region to the visiting bird. The head is tilted downward 15–25°, and the tail is erected to a 60–80° angle. The black lower back feathers and upper tail coverts are erected. The wings are drooped somewhat and vibrated very rapidly, exposing a small patch of white in the underside of the wings. This appears as a white blur bordered by the black of the rest of the wing. The crown and upper back feathers are depressed, while the pupils are contracted. A male performing this display usually remains stationary; however, when a displaying bird be-

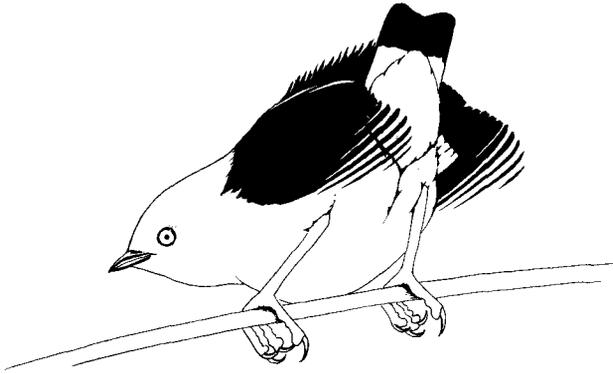


FIG. 6. Adult male performing a tail-up freeze for another bird.

comes extremely excited, he may twist from side-to-side. The performer's feet appear to remain stationary during the twisting. Very rarely, a male may back toward the visitor while performing this display.

A visiting bird is confronted with a conspicuous area of yellow as it faces the posterior of the displaying bird. This area is bordered by the black of the tail, and the vent region is accented by the black and white blur of the vibrating wings. Usually this display lasts 3–4 sec before the displaying bird initiates a swoop-in flight; however, the duration varies depending on the response of the visiting bird.

"*Swoop-in flight.*"—The swoop-in flight is initiated primarily from the main perch. In most cases, another bird is present, e.g., B1-R (alpha male of T1) performed 94% of his flights ($N = 835$) in the presence of another bird. During a solo display, the owner leaves the main perch and flies directly to a perch 15–30 m away. This distant perch is always higher than the main perch, e.g., in T1 it was 3 m higher. Upon landing at the far perch, he usually produces a *klok*; he then immediately turns around and quickly swoops downward, producing a *kloop* at the lowest point of the swoop before swinging upward to the main perch. In solo display the culminating call is invariably given the instant before reaching the main perch. As he reaches the main perch, the male quickly turns around (difficult to detect) in mid-air and lands on the perch facing in the direction from which he came. Duration of the display varies according to distance of the far perch. The flights of territorial owner 1 (B1-R) all fell within a 7–8 sec range, whereas those of territorial owner 2 (BKR) lasted 6.5–7.3 sec. Most variation in duration within a single owner's flights occurs from

the time he leaves the main perch and lands at the far perch; there is virtually no variation in the return part of the display.

“Joint display between males.”—Most displays between males involve a territorial owner and another adult-plumaged male usually familiar with the owner and his display area. Once the owner has detected another male, he may perform a few short flights and give an advertisement call or two, or rarely a butterfly display before he moves to the main perch and does a side-to-side display. After the visiting bird has been enticed to the perch, the owner may perform a tail-up freeze, but more frequently, especially among “well-acquainted” partners, i.e., alpha and beta males that have displayed together for at least several days, he will immediately initiate a swoop-in flight. This type of swoop-in flight is identical to that conducted in the absence of another bird, except that the visiting male often may give a normal display call in the interval between departure of the territorial male from the main perch and his return. Only the visiting male gives the normal display call during display bouts. The instant before a returning male gives the culminating call and lands, the passive bird may give an advertisement call just before the active male delivers the culminating call (Fig. 3b). The passive male then flies to the far perch and performs a swoop-in flight, exchanging positions with the other bird on the main perch. In well-acquainted pairs, the passive bird often will fly directly to the far perch following an exchange, and will rapidly return with a swoop-in flight. These highly-synchronized displays are very impressive and may continue for several minutes. When a pair resumes displaying after a short break, it is usually the alpha male that initiates the bout. Displays between owner and visiting adult male are not necessarily well coordinated, particularly if the visiting bird is very aggressive. In uncoordinated display the visitor may fail to bend down and fly off as the owner approaches the perch during a swoop-in flight or the visitor may fail to conduct a swoop-in flight after the alpha male has done so. In these instances, the owner will either swoop over the main perch or, less frequently, will land next to the uncooperative bird. Displays involving the owner and immature males are usually short and uncoordinated.

“Male and female interactions.”—In contrast to male-male interactions, presumed females do not join in displays and apparently almost never call while on the lek. As mentioned earlier, this behavior was used to distinguish females from immature males, as females often exhibit some male plumage characters (Graves 1981). During brief visits by female-plumaged birds, it was often impossible to determine their sex.

As with male-male interactions, the alpha male may perform several short flights, occasionally a butterfly display, and give an advertisement call or two before moving to the main perch to perform a side-to-side invitation.

After the female has been enticed to the display perch, the male usually performs the tail-up freeze. If the female should move to an adjacent perch, the male may give an advertisement call and then perform another series of side-to-side displays until the female rejoins him. He may again perform a tail-up freeze before rapidly flying from the perch to perform a sloop-in flight. In 92% (N = 59) of the sloop-in flights the female bent down and flew to an adjacent perch just as the male reached the main perch. The male will often perform a horizontal freeze immediately following a sloop-in flight, or he may perform a short flight from the main perch to a nearby perch before exhibiting the horizontal freeze. After this he may perform a butterfly display or one or two short flights. If the female has not returned to the main perch, he will move there and perform another side-to-side display. I never saw an owner pursue a female once she left his area. Usually a male performed a few short flights, or, if his regular partner was present, they would perform a series of sloop-in flights in an apparent attempt to attract the female back to the area.

In the only copulation observed, the alpha male (BKR) and the beta male (WB) performed several sloop-in flights before I detected the female. The beta male did a short flight followed by a horizontal freeze (ca. 10 sec long). The alpha male flew to the main perch while the beta male performed a few more short flights. The alpha male then did a side-to-side display. As soon as the female moved to the main perch, the alpha male immediately initiated a sloop-in flight. Upon returning he did the usual turn-around in mid-air, but instead of landing on the perch, he landed on the female's back and copulated with her for ca. 2.5 sec. During the copulation, the female was bent forward slightly (about 30°). The male rapidly flapped his wings as in a flutter display. After completion, the female flew to an adjacent perch before flying from view. The beta male joined the alpha male, and both gave a few advertisement calls.

Table 2 summarizes the conditions when calls and displays are given by alpha male *P. fasciicauda*.

COMPARISON WITHIN THE SUPERSPECIES COMPLEX

Making behavioral and ecological comparisons between closely related species pinpoints the differences that have arisen since speciation of a particular group. Such a comparison not only may reveal evolutionary pathways within a particular group, but also may elucidate general patterns of evolution of behavior.

A detailed comparison of displays can now be made between *P. fasciicauda* and *P. filicauda*, within the superspecies complex. Observations for *P. aureola* are still incomplete. Nevertheless, some notable trends can be discerned among the three species (Table 3).

TABLE 2
SITUATIONS IN WHICH ALPHA MALE *PIPRA FASCIICAUDA* CALL AND DISPLAY

	No other bird present	Another male present	Female present
Advertisement call	X	X	X
Simultaneous call	—	X	X ^a
Appeasement call	—	X	X ^a
Display call			
Normal	—	X	X ^a
Partial	—	X	—
Slurred	X	—	—
Culminating call	X	X	X
<i>Klok</i>	X	X	X
<i>Kloop</i>	X	X	X
Side-to-side display	—	X	X
Short flight	—	X	X
Stationary display	—	X	X
Horizontal freeze	—	—	X
Butterfly display	—	X	X
Aerial chase	—	X ^b	—
Flutter	X	X	X
Tail-up freeze	—	X	X
Swoop-in flight	X	X	X

^a The simultaneous call, appeasement whistle and normal display call are rarely given when a female is present.

^b In most instances, the aerial chase involves the beta and a nonterritorial male.

Vocalizations and displays are remarkably similar between *P. filicauda* and *P. fasciicauda*. Presumably, these strong similarities are shared by *P. aureola*, as *P. fasciicauda* and *P. aureola* are more similar morphologically than either is to *P. filicauda*. All three species exhibit the side-to-side display, short flight, and swoop-in flight apparently common in one form or another to all *Pipra* studied so far (Snow 1963b, Sick 1967). The orientation of a male's posterior region toward a visitor is also widespread in *Pipra*. Every species in the Red-capped Manakin (*P. mentalis*) complex (*P. mentalis*], [*P. erythrocephala*], Red-headed [*P. rubrocapilla*] and Round-tailed [*P. chloromeros*] manakins) has a black posterior that is highlighted by either bright yellow or red feathered thighs. This orientation may have led to the evolution of striking plumage patterns in the posterior region of Blue-rumped (*P. isidorei*), Cerulean-rumped (*P. caeruleocapilla*), White-fronted (*P. serena*), and Snow-capped (*P. natterei*) manakins, though little is known about the display of these species. Within the *P. aureola* complex, the differences in visual (and tactile in *P. filicauda*)

TABLE 3
COMPARISON OF DISPLAY WITHIN THE SUPERSPECIES COMPLEX

	<i>P. aureola</i>	<i>P. fasciicauda</i>	<i>P. filicauda</i>
Advertisement call	+ ^a	+	+
Appeasement whistle (includes conflict and appeasement patterns)	?	+	+
Display call			
Normal	?	+	-
Partial	?	+	-
Slurred	?	+	+
Culminating call	+	+	+
<i>Klok</i>	+	+	+
<i>Kloop</i>	+	+	+
Side-to-side display	+	+	+
Short flight	+	+	+
Stationary display	+	+	+
Horizontal freeze	?	+	?
Butterfly display	+	+	+
Flutter	+	+	+
Aerial chase	?	+	?
Tail-up freeze	+	+	+
Twist	-	-	+
Swoop-in flight	+	+	+
Coordinated display between males	+	+	+

^a +, - or ? indicates the presence, absence or uncertainty of a behavior in the species repertoire.

stimulation exhibited to a visitor during the tail-up freeze may be important isolating mechanisms. The vent region of male *P. aureola* and *P. filicauda* is primarily black, although the bright breast feathers (red in *P. aureola*, yellow in *P. filicauda*) extend narrowly into this region. In contrast, the vent area of *P. fasciicauda* is almost entirely yellow.

Unlike all other *Pipra*, *P. fasciicauda* and *P. filicauda* have unique tail patterns. The yellowish-white tail band of *P. fasciicauda* is most conspicuous when the bird gives the advertisement call. The coevolution of the elongated tail filaments and the "twist" in *P. filicauda* has resulted in one of the most unusual behaviors in the family (Schwartz and Snow 1978). Several piprids have lengthened tail feathers; however, only *P. filicauda* is known to use the modified feathers for tactile stimulation. Schwartz and Snow (1978) suggested that the twist of *P. filicauda* possibly evolved from an about-face movement, i.e., pivoting. The about-face movement is unreported for *P. aureola*. *P. fasciicauda* exhibits some pivoting (the feet do not appear to move) during the tail-up freeze. Since all three species ex-

hibit the tail-up freeze, it seems likely that the twist of *P. filicauda* may have been derived from it. Upon isolation, selection may have favored male *P. filicauda* that adopted movement during the tail-up freeze. Occasional contact between the male's tail and the female during this display may have promoted the coevolution of the long tail filaments and the twisting motion in *P. filicauda* (Schwartz and Snow 1978). Females of *P. fasciicauda* occasionally hop quite close to a male performing the tail-up freeze, almost making contact with his tail and vent region. On four occasions, immature males of *P. fasciicauda* pecked at the erected lower back feathers, tail and/or undertail coverts of an adult male during this display. Schwartz and Snow (1978) noted this same phenomenon exhibited by immature males of *P. filicauda* during the twist.

Another notable plumage characteristic restricted to the *P. aureola* complex is the presence of white in the flight feathers. This striking feature further enhances the conspicuousness of the displaying males. It is evident in all flight displays and aids in accenting the vent region during the tail-up freeze. Furthermore, the degree of coordination between displaying males of this complex is apparently unequaled by other *Pipra* and surpassed in Pipridae only by *Chiroxiphia* spp. The aerial chase is unreported for *P. filicauda* and *P. aureola*; however, this relatively rare behavior may go undetected without prolonged study. The aerial chase and the butterfly display are very similar behaviors, with both incorporating the relatively slow, conspicuous wing beat. The precursor of these displays may have developed out of conflicts between two (or more) birds when one individual chased another around or from his territory. Competing males may have adopted the slower wing beat as a means of reducing the intensity of chases. Presumably, males were gradually acquiring more conspicuous plumage, e.g., increased white in the wings. With the gradual decrease in aggression between males, allowing for the evolution of joint display, the chase behavior may have been incorporated into the nonaggressive, highly-ritualized butterfly display, with its subsequent decrease in use in conflicts. This may explain why the aerial chase is relatively rare and occurs only when there is intense competition for a territory between three or more males.

As with the aerial chase, the lack of observation of the horizontal freeze in the other two species may be an artefact of short term studies. This display may have evolved from the more generalized stationary displays, since in both displays the bird is horizontal (more so in the freeze) and anticipates the action of another bird (only females in the freeze).

The swoop-in flights of *P. filicauda* and *P. fasciicauda* differ in two notable ways. Whether in solo or joint display, male *P. fasciicauda* terminate the swoop-in flight on the main perch. The only exception is during

duets when the passive partner fails to bend down and fly as the active bird approaches the perch. In such instances, the active male will either fly over the main perch or, less frequently, will land quietly next to the passive bird. This contrasts sharply with similar behavior of *P. filicauda*, wherein usually, either in solo or duets, the performer over flies the main perch and lands on a nearby one (Schwartz and Snow 1978). In addition, male *P. fasciicauda* give only a single culminating call at the termination of a swoop-in flight. Schwartz and Snow (1978) identified two different, but quite similar, calls in *P. filicauda* that are given under different circumstances at the termination of the swoop-in flight. The first, and most frequently given, the pass-by call, is delivered by an active bird as it flies over the main perch and lands on an auxiliary perch. The second, somewhat longer version, is given when the male flies over and then veers back to the main perch.

Schwartz and Snow (1978) distinguished two types of soft, *sweee*, whistles of *P. filicauda*. Shorter whistles (<0.4 sec) were termed "conflict whistles," while longer ones (>0.5 sec) were referred to as "appeasement whistles." I recorded both short and long as well as intermediate whistles for *P. fasciicauda* that are similar to those of *P. filicauda*. The whistle is more gradually inflected upward in *P. fasciicauda*. In *P. fasciicauda* there seemed to be little distinction in context between short and long whistles, since the same individual may intermix them.

The duration of the advertisement call of *P. fasciicauda* is almost twice that of *P. filicauda*. The "normal" and partial display calls are apparently nonexistent in *P. filicauda*. However, a spectrogram in Schwartz and Snow's (1978: Fig. 3K) paper is similar to that of the slurred display call of *P. fasciicauda*. Schwartz and Snow (1978) did not determine the function of the call represented in the above spectrogram; however, since the call is apparently given under similar circumstances to that of *P. fasciicauda*'s slurred display call, it probably serves the same function, i.e., to attract birds to display. One of the calls, a double-noted *chee-weep*, described by Snow (1963a) for *P. aureola* may be a homologue of the "normal" display call of *P. fasciicauda*.

The display sites of *P. fasciicauda* and *P. filicauda* apparently differ notably. However, caution must be exercised in comparing display sites until each species has been studied under a variety of situations. The understory in *P. filicauda* leks is apparently more open than that in *P. fasciicauda* leks; in fact, Schwartz and Snow (1978:55) mention that the understory below 2–4 m at *P. filicauda* leks is particularly bare, with only "a sparse to moderately dense scattering of sapplings and vines." All display sites of *P. fasciicauda* (five different leks were visited) had dense vegetation below 2 m. Foliage density above 2 m varied from moderate to

heavy. These differences in vegetation structure may explain why the main perches of *P. fasciicauda* are consistently higher than those of *P. flicauda*. Schwartz and Snow (1978) found no *P. flicauda* territories to be contiguous; in contrast, several *P. fasciicauda* territories were contiguous. Comparison of other behavioral and ecological aspects must await more detailed studies of *P. aureola* and *P. flicauda*.

In summary, the above comparisons, particularly between *P. flicauda* and *P. fasciicauda*, further support the suggestion of Haffer (1970) and Schwartz and Snow (1978) that *P. aureola*, *P. fasciicauda*, and *P. flicauda* comprise a superspecies.

SUMMARY

Color-marked Band-tailed Manakins (*Pipra fasciicauda*) were studied for 6.5 months in undisturbed lowland rain forest of southeastern Peru in 1980. Males congregate at localized, naturally disturbed areas in seasonally flooded forest. The display of *P. fasciicauda* differs from most other manakins in that usually two or more males perform coordinated displays to attract and excite females. At each display site, an alpha male (the dominant bird) usually performs coordinated displays with a subordinate male. Once a female arrives, it is only the alpha male that actively courts her.

A male's display repertoire consists of several elaborate displays that combine visual and acoustical elements to enhance his conspicuousness to a female. The acoustical element is composed of both mechanically and vocally produced sound.

The display repertoire of *P. fasciicauda* is remarkably similar to that of *P. aureola* and *P. flicauda*. This, combined with the similarity in plumage shared by these species, supports the contention that the three species comprise a superspecies.

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COLOR PLATE

The colorplate Frontispiece of the Band-tailed Manakin (*Pipra fasciicauda*) has been made possible by an endowment established by the late George Miksch Sutton. Painting by F. P. Bennett, Jr.