

SHORT COMMUNICATIONS

Display repertoire and social organization of the White-fronted and White-throated manikins.—The ecological, behavioral, and morphological variability observed among the 51 species of Pipridae (Snow 1979) is ideal for studying evolution of leks and the effects of sexual selection on speciation (Bradbury 1981, Prum and Johnson 1987). For example, several types of spacing patterns and male strategies have been described. The best studied manakin species form “classical leks” or “true leks” (Bradbury 1977, 1981; Oring 1982) in which males holding densely grouped individual territories perform competitive displays (i.e., White-bearded Manakin [*Manacus manacus*] [Snow 1962a; Lill 1974a, b] and Golden-headed Manakin [*Pipra erythrocephala*] [Snow 1962b, Lill 1976]). In “exploded leks” or “quasi-leks” (Gilliard 1963, Bradbury 1981, Oring 1982), individual males are more widely separated than in “classical leks”; they often display in auditory rather than in visual contact from sites that appear markedly clumped only when considering total home ranges (Bradbury 1981, Oring 1982, Bradbury and Gibson 1983, Foster 1983, Bradbury et al. 1986, Beehler and Foster 1988). In “classical” as in “exploded” leks, males may cooperate to attract females, although a single dominant male engages in pre-copulatory courtship display and copulation (review in Foster 1985).

During a study of seven sympatric species of Pipridae in French Guiana, I noted that courtship displays and social organization of the White-fronted Manakin (*P. serena*, nominate sub-species) and the White-throated Manakin (*Corapipo gutturalis*) differ from the previous descriptions given by Prum (1985, 1986). I present here my observations on the mating systems of these two species.

My study was made during two years of field work including three successive reproductive seasons (1985–1987): 18 months on the “Piste de St-Elie” site (5°04'N, 53°18'W, primary forest with secondary vegetation along the track, site described in Sabatier 1985) and five months in intact primary forest around a granite inselberg (“Inselberg des Nouragues,” 4°05'N, 52°40'W, site described in Erard et al. 1989).

White-fronted Manakin.—Prum (1985) identified in Suriname “exploded” type leks in which the males, established in one well-determined area, perform both solitary and coordinated displays on their own or on another male’s territory. Since no copulation was observed, it is impossible to define the precise role of such coordinated displays in this species breeding system. However, Prum (1985) observed female visits to males during both solitary and coordinated display, and he concluded that the coordinated displays appear to be more competitive than cooperative.

In French Guiana, I color banded 25 individuals (18 adult males) on three arenas and observed five arenas (formed, respectively, by eight, six, six, five, and five males) during 48 days (475 h). I also monitored by radio-tracking the activity of six individuals during 45 days (530 h).

My observations of displays of White-fronted Manakins are similar to those of Prum (1985), with the significant addition of the full behavioral sequence leading to copulation (Fig. 1). At the approach of a female, the male first flies between two horizontal perches producing a low rustling sound with his wings, and then performs a series of rapid flights between vertical perches on which he lands facing the center of the arena. The female joins him following his flights between perches. Male and female then restrict their display to two vertical perches between which they cross each other in flight. Prum (1985) describes the same display performed by a single male or a pair of coordinated males. During my study, 87 courtship displays were observed. Copulation occurred on only three occasions, during which the male flew above the female as they crossed between perches. It is possible

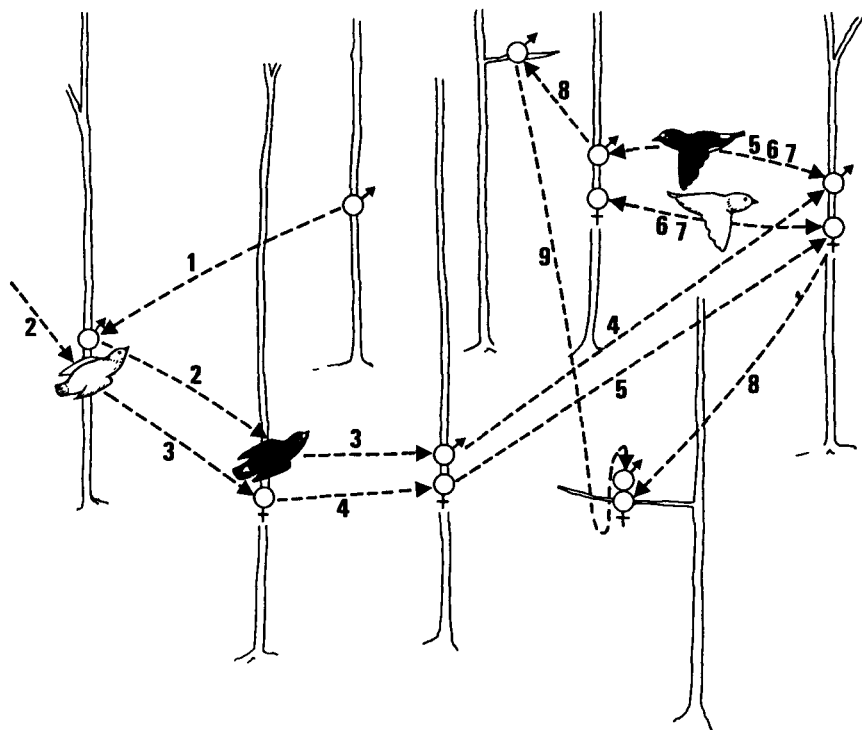


FIG. 1. Schematic representation of the *Pipra serena* courtship display: (1) Last of a series of flights by the male between vertical perches. (2 to 5) Simultaneous flights by male and female between 5 and 10 vertical perches. (6 and 7) The male and female cross each other several times in flight between perches, the male flying higher than the female. (8) The male perches above the female who has landed on the perch where copulation will take place. (9) S-shaped display flight: the male approaches the perch from below, then lands directly on the female for copulation.

that the female's lower position is a signal indicating that she accepts copulation, as in the White-bearded Manakin (Snow 1962a). The female then landed on a thin branch 1 or 2 m above the ground while the male settled on a perch above her. The male then performed a ritualized display flight tracing a horizontal S-pattern in the air (Prum 1985), approaching the nuptial perch from below, and landing directly on the female for copulation. The same display flight has been described in the Golden-headed Manakin (Snow 1962b, Sick 1967, Lill 1976). The entire behavioral sequence is very similar to the performance of the courtship display by Blue-crowned Manakins (*P. coronata*), although in *Pipra coronata* the coordinated "dance" display frequently was performed between males after the nesting season, females visited only single males.

In *Pipra serena*, coordinated displays between males are performed between an established territorial male and unrelated, non-resident males (Prum 1985). I observed in French Guiana 46 displays between males: 27 before the breeding season when adult males were establishing

their individual territories, 15 after the breeding period, but only four when the females were visiting the arenas. The males involved were mostly residents banded at the same arena during the previous breeding season ($N = 42$), unbanded adult males ($N = 22$), immature males in transitional plumage ($N = 18$) or adult males in their second year ($N = 10$). Coordinated displays frequently occurred in response to the invasion of display territories by non-resident males (46 displays for 67 invasions). On 31 occasions, the invading male followed the resident in his rapid flights among the low trees and shrubs of the understory. The territorial conflict stopped when the invading bird left the territory after the series of rapid flights ($N = 21$) or when he displayed like a female, flying lower than the resident male when they crossed between two perches ($N = 23$). On four occasions the visitor alighted momentarily on the nuptial perch of the resident male. These evidences support the conclusion of Prum (1985) that in *Pipra serena* the coordinated displays are more competitive than cooperative. Although Prum (1985) observed a female visiting a pair of displaying males, copulation in *Pipra serena* seems to occur only when females are visiting single males, as in *Pipra coronata*.

The spacing patterns of males measured during three successive reproductive seasons showed that White-fronted Manakins form "classical leks" in French Guiana. On each arena, five to eight males called and displayed in close proximity, each one occupying a 4–6 m diameter area within a 15–18 m diameter arena. The mean distance between the males and their nearest neighbor was 5.6 ± 1.2 m [SD] ($N = 35$). In addition, the lek of *P. serena* in French Guiana is not restricted to a single spot. Five groups of males systematically moved from an initial site, only used early in the day (visits of females from 6:30 to 9:30) to a second site, located 80–100 m lower down on the slope, only occupied later in the day (visits of females from 11:30 to 15:00). During the breeding season, all banded males (the 15 residents of three arenas observed during 21 days) and all radio-tracked males (three residents of different arenas followed during 24 days) showed a similar daily movement and used the same display territories. Each male defended both territories against the intrusions of unestablished males or neighbors and called throughout the day, with two periods of increasing activity when females visited the arenas. During 36 h each of three banded males was on territory 78%–86% of the day (72% to over 90% in Prum 1985). Among three copulations observed at three different arenas, two occurred in the morning between 7:00 and 9:00 (at the "morning locality") and one at 13:00 (at the "midday locality"). This displacement of the group of males appears to be linked to the intensity of light available in particular forest areas at particular times of the day. The most illuminated areas were at the tops of the slopes at dawn and farther downward in the valleys at midday. The males were moving every day from one spot to another during set display hours in order to benefit from better lighting conditions with respect to the very dark surrounding areas. Because of the regular use of two display sites by *P. serena* in French Guiana, I refer to this type of mating system as a "double-spot lek," in opposition to previously described leks which are restricted to a single spot. This terminology is independent of the dispersion patterns of males within the arena (i.e., classical or exploded leks).

These observations reveal the existence of geographic variation in *Pipra serena's* lek behavior. Prum (1985) identified "exploded" leks in Suriname, and I found "classical" leks in French Guiana. In addition, Prum (1985) observed a male singing persistently from a single territory for over 70–90% of 5-min periods distributed throughout the day, whereas I described the existence of a "double-spot lek." This geographic variation could be related to different environmental conditions in the studied localities, among which eventual differences of illumination in the understory. For example, in Suriname males could display at a single site with good light exposure all day long, whereas in French Guiana they had to move from one locality with good light exposure in the morning to a site better illuminated

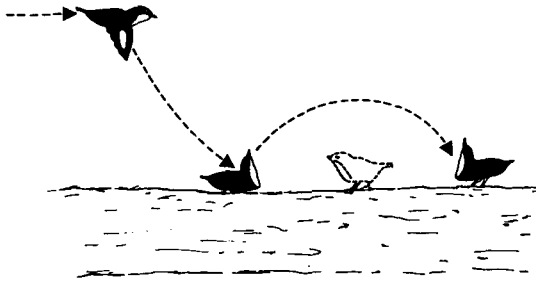


FIG. 2. Display flight of an adult *Corapipo gutturalis* above a subordinate male (dotted line). The bird points his raised throat toward the intruder, a posture he maintains for some seconds after having landed on the fallen log (cf. "performance of the display call," Prum 1986).

at midday. This evidence supports the "hotspot model" of lek evolution (Bradbury and Gibson 1983, Bradbury et al. 1986) because it suggests that males initiate the process of clumping and use two courtship locations in order to meet as many females as possible.

White-throated Manakin. — Prum (1986) described the existence in Suriname of "detached or mobile leks," based on limited observations of competitive displays by several adult and immature males together on a series of moss-covered logs. Davis (1949) observed copulation following competitive display by a group of six or more males and females. I studied six arenas in French Guiana for 57 days (610 h) distributed over three successive reproductive seasons. Five adult males, three females, and two immature males in transitional plumage were banded in a single lek. Observations were carried out when the males established their individual territories after an estratism period lasting from August to the end of September (dry season, 23 days of observation), and when females visited frequently the arenas during the breeding season (rainy season, 34 days of observation). My observations of the display repertoire of White-throated Manakins are very similar to those of Prum (1986), with the addition of the full behavioral sequence leading to copulation. However, I noted in French Guiana a context-dependent variation of fallen log displays. I observed 129 times the "performance of the display call" (Fig. 2) described by Prum (1986). This display was essentially performed between males in the absence of a female (85 times) and by solitary males (44 times), but never by a single male in the presence of a female. It was often observed when males were establishing their individual territories before the breeding period (67 displays by groups of males, 44 displays by solitary males) and more rarely during the breeding period in the absence of a female (18 times). In fact, during the "performance of the display call," the male seems to express dominance by passing over subordinate individuals and displaying his raised throat-patch toward the intruder. These observations are consistent with the descriptions given by Prum (1986): in Suriname the log-approach display, in which the male lands on the log and rebounds forward (over another individual if present) and facing back toward where he first landed (Fig. 2), was commonly performed between competitive males. In addition when Prum (1986) observed a female on a log, the male walked backward toward her immediately upon landing in a position which necessarily requires the male facing away from the other individual present and not facing toward him such as when he displayed competitively in front of an intruder.

During the complete courtship display cycle (Fig. 3), the ritualized display flight with synchronous calls ("display call," Prum 1986) and flashing of white wing-patches is followed

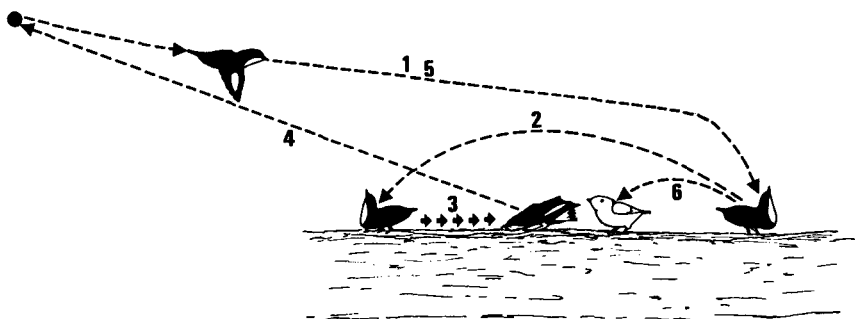


FIG. 3. *Corapipo gutturalis* courtship display in the presence of a female: (1) stereotyped display flight with synchronous calls. Landing with throat displayed to the outside, the male flaps his wings noisily, then rebounds directly backwards over the female. (2) Rebound in the direction from which he came, facing out the original direction of flight. (3) After having maintained his "bill-pointing" posture to the outside, the male creeps backwards toward the female, his throat lowered onto the log, rapidly flapping his wings alternately, flashing his white wing-patches. He approaches the female until she either touches him with her bill or flies off. (4) The male returns to his perch, in line with the log. (5) The male again performs the display flight with synchronous calls. (6) Immediately after having snapped his wings and landed in bill-pointing posture to the outside, the male drops to the female's back for copulation.

by dropping to the log, snapping the wings, and performing an about-face above the female. The male lands beyond the female with a snap of his wings (producing the "pop," Prum 1986) and rebounds toward the outside over the female. The male then walks backwards toward his partner, head down and tail up, opening his wings alternately ("slow undulating crawl," Davis 1949; "wing-shiver display," Prum 1986). The throat feathers are raised by rubbing them against the moss, the primary remiges and the rectrices pointing toward the female's head (Fig. 4). I observed 168 courtship displays by solitary males in the presence of a female. These courtships were very stereotyped and the male always performed the display call ending in a final "pop." On 128 occasions, the male landed in "bill-pointing posture" after the rebound over the female. On 40 occasions, the male began the "wing-shiver display" immediately upon the second landing. During the three displays resulting in copulation, the female touched the tips of the male's primaries with her bill at the end of the "wing-shiver display." This behavior, also observed in *Pipra erythrocephala* (Lill 1976), *P. filicauda* (Schwartz and Snow 1978), and *Rupicola rupicola* (Snow 1971) probably indicates acceptance of copulation. The male then repeats the display, starting from the ritualized display flight, and lands directly on the female after dropping to the log, snapping his wings, and performing an about-face. During the same breeding season, two copulations were performed by two different banded males using different fallen logs on the same arena. This evidence does not support the "hotshot model" of lek evolution (Beehler and Foster 1988), because different males from the same arena seemed to be equally attractive for females.

Quite obviously, the mobile group display is less important in White-throated Manakin's breeding system than exclusive territorial behavior. In my observations, the log-approach displays differ when performed competitively from when they are performed during a female visit. The white throat-patch is directed inward for competitive displays in the absence of

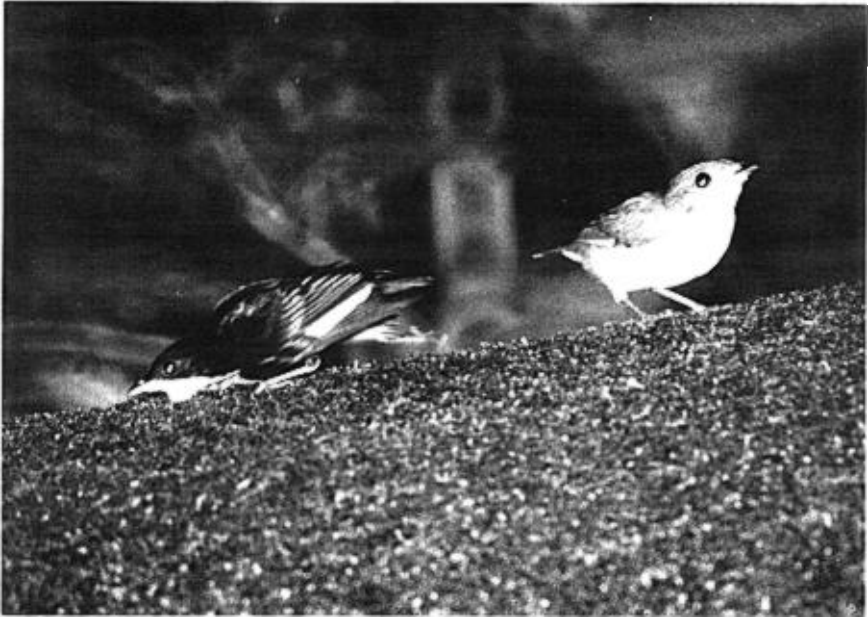


FIG. 4. Adult male *Corapipo gutturalis* "wing-shiver display" in front of a female. Walking backwards, the male rubs his throat against the moss-covered log and opens his wings alternately, displaying the three white patches in his plumage. To signal acceptance of copulation, the female touches the tips of the primary remiges with her bill.

a female (Fig. 2) and outward for female courtship with "wing-shiver display" (Fig. 3). However, competitive displays certainly have an attractiveness function in courtship behavior, since Davis (1949) observed a pair copulate immediately after a group display. Despite intensive searching I never observed or heard any flight-song display of White-throated Manakins above the forest canopy as described by Davis (1982) and Prum (1986). On the other hand, I observed on 35 occasions a different form of log approach in which a male flew from a nearby perch to the log in a slow flapping "butterfly flight." The wing-beat was very deep and so slow that the white wing-patches were clearly visible at each downstroke of the wing. This log approach, which performance by solitary males ($N = 12$) or by residents in reaction to the visit of neighboring males ($N = 23$) was only observed during the breeding season, is very similar to the display flight of White-crowned Manakins (Snow 1961, pers. obs.).

In French Guiana, the 31 display logs located were organized in five exploded leks (two on the "Piste de St-Elie" site and three on the "Inselberg des Nouragues" site). The mean distance between display logs of each arena was 38 ± 13 m ($N = 26$). Leks were about 120 m in diameter and 230 m apart. Prum (1986) found in Suriname a similar spatial organization of the display sites, even if the "exploded" leks were significantly larger and farther apart (about 250 m in diameter and 350 m apart). However, Prum (1986) concluded the existence of a "detached" or "mobile" lek was due to "the abandonment of exclusive display territories for the competitive group display at a series of sites." I agree with Davis (1949) and Prum

(1986) that females White-throated Manakins sometimes choose to visit males during group display, but I consider exclusive territorial behavior to be more important in this species breeding system than mobile group display. My observations of three copulations after single male's displays show that group display is not an absolute condition for copulation to take place. Consequently, I consider White-throated Manakins to be simply organized in "exploded" type leks.

Adult *Corapipo gutturalis* males, like *Manacus manacus* and *Pipra erythrocephala* males, occupy territories which, at set display times, benefit from better lighting conditions with respect to the surrounding areas (Théry 1987). In *Pipra serena*, the daily variations of light exposure in the understory could lead to the regular movement of males in a "double-spot lek." The type of lek used by different species (classic or exploded, single- or double-spot) may be determined in part by environmental conditions (spatial and temporal distribution of food resources, availability of appropriate display sites) as well as by size of the ranges of the males and females.

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Lead concentrations in Golden and Bald eagles.—In recent years, lead (Pb) was found in elevated concentrations in free-ranging Bald Eagles (*Haliaeetus leucocephalus*), sometimes in high enough quantities to cause mortality (Kaiser et al. 1980, Reichel et al. 1984). Published reports of mortality due to lead poisoning in other free-ranging raptors are few. California Condors (*Gymnogyps californianus*), Rough-legged Hawks (*Buteo lagopus*), Golden Eagles (*Aquila chrysaetos*), and a Red-tailed Hawk (*Buteo jamaicensis*) have died due to lead poisoning (USFWS 1985, Wiemeyer et al. 1988). Additionally, other Golden Eagles which died from diseases or unknown causes contained elevated lead concentrations (USFWS 1985). We report lead concentrations in the livers of 16 Golden and six Bald eagles and in blood samples from two Golden and two Bald eagles found dead or moribund in Idaho.

Study area and methods.—From 1977 through 1984, the Idaho Department of Fish and Game (IDFG) sent eagles to the National Wildlife Health Research Center (NWHRC),