

## Social Organization and Behavior of the Swallow-tailed Manakin, *Chiroxiphia caudata*

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The study of interactions among members of avian species with different social systems has been an active area of research in the past decade for several reasons. First, by considering the evolutionary implications of such interactions, it often is possible to elucidate the forces molding the system. Secondly, such studies increase our understanding of the ways and circumstances under which different types of evolutionary processes may function. Particularly important is the comparison of the ecologies of species with different systems, so that factors that may have influenced the evolution of such systems may be identified. Manakins (family Pipridae) are especially suitable for studies in this area because of the wide variety of reproduction and life history strategies they exhibit. The family includes monogamous species, species in which polygynous males have random or dispersed distributions through the habitat, and promiscuous species in which males congregate at traditional sites (leks) to display for females. The species most highly evolved socially are those in which the males engage in displays requiring the participation of more than one individual. Because the males performing these cooperative displays are sexual rivals, the evolution and persistence of such behavior is of interest.

The four species of the manakin genus *Chiroxiphia* all exhibit cooperative courtship. In an attempt to explain the evolution of such behavior and the social systems associated with it, I initiated a comparative study of the social behavior, breeding biology, and feeding ecology of these forms. Three of the species (*C. linearis*, *C. lanceolata*, *C. pareola*) are very similar morphologically, vocally, and behaviorally, and form a close-knit

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species group. All have coordinated dances involving 2 or 3 males. My field study of marked individuals of *C. linearis* (Foster, 1977) showed that a group of display perches in a single court is owned by a pair of males whose association persists from one to several years. One male is dominant, a position he retains throughout the association. The dominant performs all copulations with any females attracted to the court. The system apparently is maintained by selection operating at the level of the individual. The subordinate male of the pair is more likely to become dominant on a court with the loss of his partner and, thus, to be reproductively successful, than is a solitary male.

Displays of *C. pareola* have been studied (Snow, 1956, 1963, 1971; Gilliard, 1959), but with few or no marked birds. Data suggest, however, that a dominance hierarchy may exist among individuals using a display perch, though the relationship among various males and the persistence of any association that may exist is unknown. The limited data available on *C. lanceolata* (Aldrich and Bole, 1937; Friedmann and Smith, 1955; Wetmore, 1972), a species geographically and morphologically intermediate between *C. pareola* and *C. linearis*, suggest that its displays and social structure are similar to those of the other two species.

The most widely disparate species in the genus—morphologically, vocally, and behaviorally—is *C. caudata*, the Swallow-tailed Manakin, which occurs in Paraguay, northern Argentina, and southeastern Brazil. Several descriptions of the communal displays of this species appear in the literature (for example, see Holt, 1925; von Ihering, 1936; Mitchell, 1957; Sick, 1959a, b; Snow, 1976), but they differ in many respects, and none is based on observations of marked birds. In an attempt to remedy this situation, I undertook a study of the social systems (Foster, 1981), breeding biology, and ecology of this form.

From September 29 to November 17, 1976, and December 4, 1977 to January 13, 1978, I studied *C. caudata* at El Tirol, 19.5 km by road north-northeast, of Encarnación, Itapúa, Paraguay. Limited additional observations were made August 31 to October 12, 1978, October 1 to 13, 1979, and August 17 to 28 and September 23 to November 2, 1980. Fieldwork conducted in 1977-1978 was supported by a grant from the National Geographic Society. Field assistance was provided by Robert E. Jones. Stephen F. Smith and John L. Strother identified the plants.

The main study area consisted of approximately 50 ha of forest adjacent to Hotel El Tirol de Paraguay (elevation, 170 to 260 m). The site was connected with other areas of forest via forest corridors adjacent to creeks. Additional patches of forest (>50 ha) were present in the area but separated from one another by cultivated areas. One of these, approximately 0.75 km from the hotel, formed a second study site. The Tirol area

lies in a zone of temperate moist forest. The weather is cool in the winter months of May through July, with highest temperatures occurring from October through March. Rain falls every month, but October, November, and December are usually the wettest months, and July, the driest.

Observations were made on birds that had been mist-netted and banded with unique combinations of three colored, celluloid leg rings. Young males, females, and a few adult males were laparotomized to determine reproductive condition. A few individuals were collected for the examination of stomach contents. Feces of netted birds were saved for analysis, as were those collected periodically under display perches.

## RESULTS

### DISPLAY BEHAVIOR

The male Swallow-tailed Manakins I studied exist in groups of 4 to 6. The group occupies a large (ca. 35-ha) area, the arena, that contains as many as 5 active display courts, each of which may contain several display perches. Males generally stay together at a particular court, instead of dispersing among several, and usually use only 1 or 2 commonly. Within groups, males are ranked in a linear dominance hierarchy (see below). The alpha or top-ranking male occupies a high calling perch (ca. 5 to 8 m up) at the court, from which he continually makes a call that sounds like a "ptuwa ptuwa." Occasionally, he is joined in a calling bout by the second-ranking, or beta male. The other males perch quietly in the understory. If a female is attracted to the court, the males all give a second call, a long, drawn out, many-times-repeated "ptawoo." They fly rapidly around the area and appear quite agitated. The two top-ranking males present at the court at that moment, usually the alpha and beta males, move to the main display perch. Usually this is a horizontal vine or branch in a small sapling that is 1 to 2 m off the ground. There, they perform the cooperative courtship display for the female. Generally, only 2 males (rarely 3) display at a time, and right to display is determined by rank.

During the courtship display, the female perches at one end of the display branch. The 2 males perch one behind the other on the same branch, oriented parallel to its length and facing her. They then execute a cartwheel-like Jump Display. The male nearest the female leaps into the air and flies toward the female. He hovers in front of her giving a raspy "buzzee" call, then turns, and flies to the far end of the branch where the second male originally was perched. In the meantime, the second male has moved forward to the front of the perch to jump, hover, and buzz.

The males alternate this behavior describing a circular path in front of the female; a sequence may include as many as 150 jumps. As the display progresses, the birds become increasingly excited. The males move faster and faster, and the diameter of the circle they describe decreases. The female hops up and down, flicks her wings, and pays close attention to the males. The dominant male terminates the display when he jumps into the air and, instead of facing the female, turns toward the other male(s) on the display perch, hovers in front of him, and gives a very shrill, high-pitched "final call." The other male assumes a submissive posture bending far over the display perch. After a few moments, the subordinate flies to a perch in the adjacent vegetation while the dominant begins a Solo Precopulatory Display for the female. In this display the male makes a series of perch changes in an irregular path around the female; periodically he stops to bow, bending and rising with stiff, jerky movements. If the female is receptive, the display is followed by copulation, which takes place on the display perch.

Birds will occasionally initiate the Solo Precopulatory Display without a preceding Jump Display, and sometimes a female leaves the court during or after the Jump Display, only. The normal display sequence, however, includes both segments. Data indicate that when the Jump Display is included, the probability that copulation will occur is increased.

#### RELATIONSHIPS AMONG MALES

The composition of the group of males occupying an arena is fairly consistent throughout the breeding season and from year to year. The linear dominance hierarchy that exists among them is determined by means of aggressive interactions that take place in the absence of females. Success in these interactions and, thus, rank, appears to be related to age, with the oldest males occupying the top positions. Males generally join a lek their first year and move up in the hierarchy as males above them are eliminated. Position in the hierarchy is stable throughout the season, between years, and from court to court. Right to display for the female and to copulate are related to rank. The males that display for females are the two highest ranking individuals present. Likewise, only the dominant male copulates. On the rare occasion when a subordinate attempted the Solo Precopulatory Display for a female, he always was interrupted and displaced by the dominant.

Because all copulations are performed by the dominant male, one wonders what the selective advantage to the subordinate of his participation in the Jump Display may be. A cooperatively displaying male may increase his fitness in several ways. First, he may be able to steal copulations. Certainly, his proximity to a receptive female is increased and his

behavior stimulatory. Two females do occasionally visit a display court simultaneously, and a subordinate may be able to copulate with a second female while the alpha male is occupied with the first. This has not been observed, however. Second, the increased experience at displaying acquired by a subordinate may contribute to his reproductive success when he is dominant or to his maintenance of a high position in the dominance hierarchy. An additional, delayed benefit may accrue if females return to leks in subsequent years as a result of a previous positive experience at the site. In this case, anything a subordinate, who eventually may be dominant, may do to increase the probability of a female's returning for mating in subsequent years will be to his advantage. Finally, subordinate males could increase their inclusive fitness through kin selection even in the absence of copulation. At present, however, no data are available on the kin relationships of the *C. caudata* males that comprise groups.

#### NESTING

I discovered one nest containing three eggs on the morning of December 4, 1977. I observed the nest briefly on December 4 and 5 and checked it from a distance with binoculars every few hours on both days. I never saw a bird in attendance. I assumed the nest was a *C. caudata* nest, however, because of the marked similarity of it and its contained eggs to those described elsewhere for the species (Burmeister, 1856; Euler, 1900; Nehr Korn cited in von Ihering, 1900; von Ihering, 1902; Chubb, 1910) and to those of other species in the genus that I have examined (Foster, 1976). When I examined the nest at 0755 on December 6, the eggs had been destroyed by a predator. The nest was more or less intact, containing pieces of eggshell and some wet egg remains. The egg remains smelled rotten, indicating that the eggs probably were addled and had been abandoned prior to predation.

The nest was located in a small (height=2 m; dbh=13 mm) tree of *Actinostemon concolor* (Spreng.) Muell.-Arg. (Euphorbiaceae), perhaps the most common species in the understory of the forest. The tree was shaded and received no direct sunlight. The nest was located 10 cm from the trunk and 88 cm above the ground. It hung from a fork in a horizontal branch between twigs 3 and 5 mm in diameter.

Inner and outer depths of the nest were 50 and 56 mm, and the inner and outer diameters, 47 and 65 mm, respectively. The outer layer of the nest was formed by black fungal hyphae (*Marasmius* sp., Agaricaceae; see Sick, 1957) to which a complete cover of *Selaginella* sp. (Selaginellaceae) was attached. The nest was lined with small twigs and brown, dry mid-ribs of leaves, wound circularly. The nest was attached to its supporting twigs with fungal hyphae and a few loosely wound, widely spaced twigs.

The eggs were pale creamy tan with brownish purple markings concentrated at the large end. One egg measured 22 x 17 mm.

#### DIET

Like many lek-breeding birds, *C. caudata* is primarily frugivorous. Although manakins may feed in trees found on the display courts, they usually feed elsewhere. Absences usually last a few minutes. I made no attempt to follow birds on their foraging trips, but observed feeding incidental to other work. Manakins feed by hovering in front of a fruit and plucking it, by perching near a fruit and reaching over and plucking it, and by flying toward a fruit and snatching it on the wing. The bird usually returns to its perch before swallowing the fruit whole. Seeds are regurgitated or passed through the gut intact, depending on their size and shape.

I identified the type of item being eaten during 28 feedings. In 22 instances (76%) the bird ate a fruit. Once the food item was a spider, twice an insect larva, and three times an adult insect. Contents of 27 of 28 (96%) stomachs examined that contained food included fruit. Two stomachs contained one spider each. In contrast to these data, regurgitation and fecal samples showed no evidence of invertebrate material. Three times I saw birds regurgitate seeds, and seven fecal samples showed evidence of fruit only. The fecal material obtained from under display perches included a total of 303 seeds, but no animal material.

*C. caudata* is primarily frugivorous although the degree to which it also feeds on invertebrates is not clear. Observations of feeding, most of which were made at the court, may overestimate the invertebrate component since fruit was less available there than elsewhere. In contrast, analyses of droppings and stomach contents may underestimate the proportion of invertebrates in the diet because identifiable remains, particularly of small, soft-bodied forms (such as larvae), may be less persistent or recognizable than fruit remains.

Plant species whose fruit was eaten by manakins during September through mid-January included:

#### Lauraceae

*Nectandra saligna* Nees and Mart.      October, November

#### Moraceae

*Cecropia* sp. (possible *C. adenopus* Mart.)      December, January

*Ficus* sp.      December, January

*Sorocea bonplandii* (Baill.) W. Burger et al.      October

#### Meliaceae

*Trichilea catigua* Adr. Juss.      October, November

#### Euphorbiaceae

*Alchornea iricurana* Cosar      October

Aquifoliaceae	
<i>Ilex paraguariensis</i> St. Hil.	October, November, December
Sapindaceae	
<i>Allophylus edulis</i> (St. Hil.) Radlk.	September, October
Flacourtiaceae	
<i>Casearia silvestris</i> SW	September
Myrtaceae	
<i>Eugenia uniflora</i> L.	September, October, November
Araliaceae	
<i>Dendropanax cuneatum</i> (D.C.) Decne. & Planch.	October, November, January
Rubiaceae	
<i>Psychotria carthaginensis</i> Tacq.	September, October, November
<i>Psychotria</i> sp.	September, October, November

In addition birds ate fruits from at least 10 unidentified species. The species most commonly represented in my sample was *Allophylus edulis* which is the staple food item when it is in fruit. *Ficus* sp. and *Cecropia* sp. were also heavily used, and *Nectandra saligna* was commonly represented.

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