Behav Ecol Sociobiol (1981) 9:167–177

Behavioral Ecology and Sociobiology

Cooperative Behavior and Social Organization of the Swallow-Tailed Manakin (*Chiroxiphia caudata*)

Mercedes S. Foster*

Department of Zoology, and Museum of Vertebrate Zoology, University of California at Berkeley, Berkeley, California, USA

Received January 8, 1981 / Accepted July 7, 1981

Summary. The mating system of the Swallow-tailed Manakin (*Chiroxiphia caudata*) is a type of non-resource based polygyny in which males aggregate at traditional sites or leks to perform cooperative displays. Each lek and all its contained courts are used communally by a group of 4–6 males. Within the group a linear dominance hierarchy exists. Position in the hierarchy persists within and between years and at all courts and is inherited in linear sequence. The dominant male of the group behaves as a sentinel calling repeatedly from a high perch in an attempt to attract females to a court.

When a female arrives, two or three males engage in a cooperative precopulatory dance, the Jump Display. This is followed by a Solo Precopulatory Display performed by a single male who, if successful, will copulate with the female. With rare exception, the dominant male performs all Solo Displays and all copulations.

Display sequences that include both a Jump Display and Solo Precopulatory Display are more likely to lead to copulation than those consisting of only one part. Thus, the subordinates who help the dominant perform the dance are expending energy that increases his fitness without receiving any immediate benefit themselves. Several factors that may have contributed to the evolution of the mating system and cooperative displays of this species are considered.

Introduction

Studies of cooperative breeding systems in birds generally deal with helping behavior at the nest (e.g. Skutch 1935, 1961; Brown 1978; Emlen 1978). Cooperation need not, however, be confined to these activities but also may involve mate attraction and courtship. This seems to be the case among the four species of the genus *Chiroxiphia* (Family Pipridae, manakins). All perform highly specialized courtship displays that are executed usually by two or three males jointly (Aldrich and Bole 1937; Friedmann and Smith 1955; Gilliard 1959; Snow 1963; Wetmore 1972), participation by at least two males being required. In *C. linearis*, males form permanent pairs and display to attract and excite females for copulation (Foster 1977). The participation of the subordinate(s) in the displays contributes to the reproductive success of the dominant partner who performs all copulations.

In this paper, I describe the cooperative display of *Chiroxiphia caudata*, the Swallow-tailed Manakin, and the social relationships and spacing patterns of the males that perform it. I then evaluate the possible functions of the display and explore factors that may have contributed to the evolution and maintenance of the behavior and its associated social system.

Materials and Methods

The Swallow-tailed Manakin is a small, largely frugivorous passerine (average weight ca. 22.75 g) in which adult males and females are strikingly dichromatic (described in Meyer de Schauensee 1970). Subadult males, which represent several year classes, are a varied mixture of adult male and female colors.

The species occupies moist forests in eastern Brazil, eastern Paraguay, and northwestern Argentina (Olrog 1959; Meyer de Schauensee 1970). I studied this species at El Tirol, 19.5 km by road ± NNE Encarnación, Dpto. Itapúa, Paraguay, from 29 September – 17 November 1976, and 4 December 1977 to 13 January 1978 (referred to as '1977' throughout the text). Limited additional observations were made between 31 August–12 October 1978, 1–13 October 1979, and 17–28 August, 23 September–2 November 1980.

The El Tirol area lies in a zone of warm temperature moist forest characterized by a moderate rainfall fairly evenly distributed through the year. Annual temperatures show somewhat greater fluctuations in the winter months of July–August, and in extremely

---

* Present address: Museum Section, US Fish and Wildlife Service, National Museum of Natural History, Washington, DC 20560, USA

0340-5443/81/0009/0167/$02.20

cold years may occasionally drop below freezing. The main study area consisted of approximately 50 ha directly adjacent to Hotel El Tirol de Paraguay. The area has never been logged though selected trees have been cut. The forest covers the moderately steep hillsides of a drainage system encompassing a number of northeast and eastward flowing creeks and having an elevational range of ca. 170–260 m above sea level. This site is connected with other areas of similar habitat via corridors of forest adjacent to the creeks. Additional large patches of forest (> 50 ha) are present in the immediate vicinity but often are separated from one another by equally large tung orchards, manioc fields, pasture, etc. A second study site was located ca. 0.75 km away in an area of flat or very gently sloping forest (elev. 210–250 m). I observed three leks within these areas, though I concentrated on individuals at the Tirol Lek, a traditional display area in the Tirol forest. At any one time this lek was occupied by a total of 4–6 males.

Birds were mist-netted and marked with three colored celluloid leg bands in unique combinations. Young males, females, and a few adult males were laparotomized to verify sex and to determine reproductive condition. This had no apparent long-term effect on the individuals involved though males usually were absent from the lek for 3–5 days following capture. Testes volumes were estimated using the formula for the volume of an of an ellipsoid, $v=\frac{4}{3}\,ab^2$, where a was half the length of the testis and b the radius at its widest point.

Results

1. Location and Use of Courts

Swallow-tailed Manakins have a modified lek/arena system in which males congregate at traditional display areas. The density of such areas was about one every 30–35 ha. Lek areas are large, and the courts within them widely dispersed (exploded lek of Gilliard 1963) so that individuals on different courts maintain auditory (rather than visual) contact or no immediate contact with one another. The Tirol arena covered ca. 9 ha though some parts of this area were much more heavily used than others. It included six main courts (usually only four in use in any given year) and several accessory display sites used occasionally. Within each court were a number of display perches upon which most of the displays were performed. These consisted of low, horizontal vines or unobstructed branches in small trees (Foster, ms).

In *C. caudata*, the entire lek is used by the group of males as a whole. No manakins (nor other birds) were actively excluded from the lek or any court, and they even were allowed to occupy the display perches as long as females were not present. Within this loose arrangement, one or two courts served as the focus of most of the lek activity though the favored courts changed during the study period. Table 1 lists for each year the number of days during which the courts were visited and the percentage of those days on which manakins were present and calling and/or displaying at each court.

Table 1. Relative use of courts on the Tirol Lek. Numbers given are percentages of the days when the courts were visited that manakins were present. In parentheses: number of days visited

Year	Courts					
	I	II	III	IV	V	VI
1976	68 (28)	30 (27)	75 (36)	100 (33)	–[a]	–
1977[b]	0 (17)	76 (17)	47 (17)	100 (34)	–	–
1978	12 (8)	10 (10)	0 (5)	50 (16)	100 (16)	–
1979	0 (6)	33 (6)	33 (6)	33 (6)	100 (8)	–
1980	0 (7)	0 (10)	85 (14)	37 (19)	100 (19)	63 (19)

[a] Court V first occupied in 1978, court VI in 1980

[b] Includes 1–13 January 1978

Birds spent nearly all their time at the favored court(s), but the frequency with which different courts were used and the number of courts visited by particular individuals varied between years. This is illustrated by the activities of KPK, an adult male present at the Tirol Lek in 1976–1977. In 1976 he was seen only at Court IV whereas in 1977 he was seen both at Courts II and IV, though most of his time was spent at IV. On 15 December 1977, Courts II and IV were observed from 05:40 – 19:20. From 05:40–17:03, KPK was present at Court IV for 9 h 41 min and at II for 30 min. The remaining 72 min can be accounted for in part by travel time between the two sites (ca. 295 m apart on a direct line) and in part by time spent at feeding areas away from the courts. It is likely that KPK would have spent even more time at Court IV, but at 17:03 he was netted (but not laparotomized). After his release, he was not seen again until the next day.

Whenever a favored court was visited, occasionally one, but usually several, manakins were present and calling or appeared within only a few moments. In addition, most male agonistic interactions and reproductive displays occurred at these sites. Court IV was favored at the Tirol Lek in both 1976 and 1977, and always was occupied during those years. In 1978–1980, a new court, V, was used most often. Court I was quite active in 1976, birds visiting it regularly between 29 September and 5 November. From 6–17 November, no birds were observed there, nor were any seen there in 1977, 1979, or 1980. Birds called there occasionally in 1978. Court III was not used in 1978, nor was court II in 1980. Court VI was added in 1980.

Because I concentrated my observations at courts with the greatest activity, my data obscure the fact that the courts differed drastically in the amounts of time they were occupied each day. This is illustrated by the 13 h 40 min of simultaneous observation made at Courts II and IV on 15 December 1977.

(These courts were selected because they were the most frequently used in 1977 and because their locations allowed observers to hear manakins calling at Courts I and III). During this time, two of the four manakins occupying the Tirol Lek plus an unidentified individual visited Court II singly or together on 11 occasions for a total of approximately 1 h and 54 min. They called but did not display. At Court IV birds were present for 11 h 11 min. This figure was artificially reduced by the netting of KPK and a female at 17:03. They and the other manakins present left the area as soon as they were released, and the court was deserted for 98 of the next 107 min. No manakins were heard calling at Courts I or III.

2. *Cooperative Behavior*

At any one time 1–6 males may be present at a particular court. Though they engage in vocal interactions and male-male aggressive displays, most commonly, a single sentinel male calls steadily from a high perch (3–12 m) in the center of the display area. The call most frequently given (phonetically resembling a *ptuwa*) is repeated ca. 9–20 times/min with bouts lasting from a few minutes to half an hour or more. The call sometimes is given antiphonally by two males. It advertises the presence of the male at the court and attracts females. The arrival of a female is heralded by the frenzied calls of the first male that sees her; this serves to alert and assemble the males in the area who call while flying rapidly around the display area making a mechanical whirring noise. At this point, one of two things happens. Most commonly (24 of 37 observations), the female and either two or three males move to a display perch where the males perform a Cartwheel Type Jump Display for the female. It is this display that requires the participation of at least two individuals though it may be performed by three (Sick 1967; Snow 1976; this study) or more (Ihering 1936; Vigil 1973). The female perches at one end of the display branch; the males, one behind the other, perch parallel to its length, or across it at ca. 30°, facing her. When the display begins, the male nearest the female jumps into the air flying toward but to the side of the female. He hangs suspended in the air facing her and very rapidly beating his wings before turning and flying (or sometimes flying backwards) to the position on the display perch originally occupied by the bird farthest from the female. When he jumps, he gives a raspy *buzzee* call. While the jumping male does this, the bird(s) in position(s) two (and three) moves forward taking over position(s) one (and two, respectively). These birds usually are bent almost horizontal and rapidly vibrate their tails in a vertical direction. Each bird, in turn, repeats this display describing a circular path in front of the female. Jump sequences may include from one to 150 jumps, being continually interrupted and reinitiated by the performers themselves (sometimes by the female). When interrupted, the males generally fly from the display branch and then return almost immediately. The female usually stays in place. As the display sequence proceeds, the jumps get faster and faster, the diameter of the circle described gets smaller and smaller, and the males appear more agitated. The female also becomes visibly excited, hopping up and down, wing-flicking, and switching her attention rapidly back and forth between males.

The display is terminated when one male, beginning the Jump-*buzz* sequence, turns in mid-air and faces the other male(s) with his back or side to the female. He hangs in the air, his wings beating very rapidly, and moves very slightly toward and then away from the other male(s), giving a shrill, high-pitched final call. While he does this, the male(s) on the display perch cowers in a submissive posture bending far forward with his tail in the air and his head level with or below one side of the display branch. The bird giving the final call immediately flies to an adjacent vertical perch. After 5–20 s, the male(s) on the display perch leave(s), and the first individual begins a Solo Precopulatory Display for the female. This display consists primarily of repeated perch changes along an irregular path around the female and series of stiff, jerky bows. If successful, copulation follows on the display perch. Although only two or sometimes three males are involved in the Jump Display, others often perch within 1–2 m of the display branch watching the display. They and the males displaced during the Jump Display remain to observe the Solo Precopulatory Display and copulation.

The alternative to this (13 of 37 observations) is for one male immediately to perform the Solo Precopulatory Display for the female without any preceding Jump Display. In four instances, a Jump Display had been performed within the previous $2^1/_4$ h. Three other times, the male performing was the only one present, and so no partner was available for the dance. In the others, partners were available but not involved, and in two of these, other males attempting to display were chased away.

I indicated above that the Jump Display serves to excite the female for copulation. However, the failure of males to perform this display in six instances when partners were available raises the questions of whether it really does serve an excitatory function and, if so, whether that excitation is necessary for copulation to occur. An alternative hypothesis is that

Table 2. Precopulatory display sequences of *Chiroxiphia caudata* and their results. In parentheses: total number in category

	n	%
Jump display only (10)		
Disrupted by other male(s)	3	30
Female left	7	70
Copulation	0	–
Jump display with immediate solo precopulatory display (9)		
Disrupted by other male(s)	1	11.1
Female left	2	22.2
Copulation	6	66.7
Jump display with delayed solo precopulatory display (4)		
Disrupted by other male(s)	1	25
Female left	1	25
Copulation	2	50
Solo precopulatory display only (9)		
Disrupted by other male(s)	1	11.1
Female left	6	66.7
Copulation	2	22.2

it serves an aggressive function ultimately determining which male copulates with the female. However, again, the failure of males to perform this display in six instances when other males were present implies that it is not necessary for the determination of dominance. Because the possibility of this latter function can be evaluated better if we first know something of the relationships among males at a lek, I delay discussion of this question until the section on male-male relationships and concentrate here on the Jump Display as an excitatory behavior. It should be emphasized, however, that these functions need not be mutually exclusive.

a) Excitatory Function. Because excitation of the female for copulation appears to be the function of the Jump Display in *C. linearis* (Foster 1977, unpubl. data), it is tempting to assign it this function in *C. caudata* also. Moreover, several types of evidence support this idea. First, this display is performed only in the presence of females. Second, the display visibly excites the female for whom it is given. When a female initially lands on the display branch, she perches erect, alertly watching the males perform. As the dance progresses, she obviously become increasingly agitated, jumping up and down, hopping rapidly from side-to-side while flicking her wings, occasionally flying to adjacent perches and back, and always closely following the action of the males.

Additional support is obtained from an analysis of the success of males in achieving copulation following different sequences of pre-copulatory display. I observed 32 undisturbed visits by females to the Tirol Lek that resulted in some precopulatory display. These displays and their outcomes are summarized in Table 2. It is apparent, first of all, that a complete display sequence, i.e., one including both the Jump Display and the Solo Precopulatory Display, is not absolutely required for copulation to occur. However, the probability of copulation is greatly increased when a complete display sequence is used. For example, 66.7% of the Solo Precopulatory Displays immediately preceded by a Jump Display and 50% of those preceded by a display 1.5–2 h before led to copulation. Only 22.2% of those not preceded by a Jump Display on the same or previous day did so, and once, when male KPK attempted to copulate with a female following a Solo Display only, she flew out from under him, and copulation did not occur. Likewise, no Jump Displays not followed by the Solo Display led to copulation. In fact, the numbers of copulations (Table 2) is significantly related to the type of precopulatory display sequence [*G*-test (Sokal and Rohlf 1969), $P<0.005$, $G=13.212$, 3 d.f.]. This also is true when data for the complete sequences are combined ($P<0.005$, $G=12.892$, 2 d.f.). Thus, it appears that the Jump Display, when included as part of a complete sequence, does result in increased numbers of copulations. This also means that the male(s) assisting in the display but not copulating does enhance the reproductive success of his partner.

Despite this, the differences between copulatory success following complete and incomplete displays could be explained in another way. It is possible that both copulation frequency and performance of complete and incomplete displays are time-related and that bouts of incomplete display were given only during periods when females were not receptive. To test this, I examined the time of day at which copulation and the various display sequences occurred. Females visited the lek between 08:00 and 18:00. However, visits were concentrated between 09:00 and 15:00, and copulation was observed only during this period (Table 3). Assuming that females were receptive at least between those hours, I compared the frequency with which copulation occurred following complete and incomplete display sequences. During that period, 8 of 12 complete sequences (66.7%) led to copulation, while only 2 of 19 incomplete sequences (10.5%) did so, indicating a relationship between type of sequence and probability of copulation independent of time of day ($P<0.005$, $G=8.312$, 1 d.f.).

b) Disruption of Displays. Many display bouts are unsuccessful because of disruption by other males (Table 2). Disruption involves several types of behav-

Table 3. Timing of female visits, copulations, and complete and incomplete display sequences by *Chiroxiphia caudata* at the Tirol Lek

Time[a]	No. ♀ visits	Copulations	Complete displays[b]	Incomplete displays
06:00	0	–	–	–
07:00	0	–	–	–
08:00	1	0	1	0
09:00	6[c]	2	1	3
10:00	5[c]	0	2	2
11:00	9	3	4	5
12:00	8[c]	3	3	5
13:00	2	1	1	1
14:00	4	1	1	3
15:00	0	–	–	–
16:00	0	–	–	–
17:00	1[c]	–	–	–

[a] One hour intervals beginning at the time indicated

[b] Jump Display with delayed Solo Precopulatory Display recorded at the time of the latter

[c] Includes females visits without display or disturbed by the author

ior. Occasionally, the individual giving the Solo Precopulatory Display is displaced by a male who prevents him from continuing his display and either forces him to join in a Jump Display or takes over the Solo Display himself. Once, a male giving the Solo Display broke off to chase a male perched in the adjacent vegetation. While he was gone, the female left. In another type of disruptive activity, one bird repeatedly tries to participate in a Jump Display already in progress. The other males repeatedly interrupt their dance to chase him away. More strikingly, the interfering bird flies directly into the middle of the dancing males, scattering them and in some instances knocking them off the perch. Such activity causes an attenuation of the Jump Display. If it continues for some time, the female leaves. Three disrupted sequences lasted from 11–21 min ($\bar{x}=13$) before the female departed, whereas the average display in sequences proceeding to the Solo Precopulatory Display lasts only 4.2 min ($n=8$; range $=1$–9).

In total, six of the 32 encounters monitored were disrupted. Of the nondisrupted displays, 38.5% led to copulation. Thus, disruption potentially decreased the number of successful copulations by ca. 18.7% (32 × 38.5%, total copulations would have numbered 12.3 instead of 10). On the other hand, Solo Precopulatory Display in the absence of Jump Display leads to copulation much less frequently (22.2% of all sequences or 25% of those without disruption) than do sequences with a Jump Display (8 of 23 = 34.8%). Thus, inclusion of the Jump Display potentially increases the number of copulations by 39.2% [(34.8% − 25%)/25%]. In this particular trade-off, therefore, the benefits of the Jump Display outweigh its costs even though these values have been calculated in the most conservative manner, i.e., so as to minimize the differences. (For example, if these percentages are calculated on the basis of the entire sample, 32, then sequences with a Jump Display lead to copulation 25% of the time whereas sequences without it do so only 6.25% of the time.) Interestingly, disruption is not significantly related to whether the display sequence includes a Jump Display or not ($G_{\mathrm{adj}}=0.095$). Some 17.4% [4] of the sequences with a Jump Display were disrupted, while 18.2% of those without one were disrupted (Jump Displays with delayed Solo Displays were included in both groups). The disruption itself occurred during three Jump Displays and three Solo Precopulatory Displays.

3. Male-Male Relationships

To clarify the nature of the relationships between males, I concentrated my observations on the 4–6 individuals consistently present at the Tirol Lek. In 1976 these included one first-year bird, one 'young adult,' and four full adults. One adult died accidentally in 1976. In 1977 only four birds were present continuously, three adults from the year before and one new subadult. However, an unbanded first-year male also visited regularly. By the end of the 1977 field season, all of the banded males had been removed. But, a new, unmarked adult began visiting the area just before this. In 1978 the Tirol Lek was occupied by four new birds, three adults and one subadult (possibly the unbanded first-year male from 1977). The two banded individuals both died accidentally. By 1979, the lek was again occupied by one adult, two subadults, and one first-year male. In 1980, two adults (one who was present as a subadult in 1979), one subadult (present as a first-year in 1979), and at least two first-year males were present regularly.

From observation of these birds, I determined that

1. though a variety of males may occasionally visit an arena, it is occupied consistently by a core group of males that is present throughout the day during an entire breeding (observation) season. Although observations were disrupted somewhat by removal experiments and accidental deaths, the core males appear to persist to a large extent from year to year as well. For example, three of the six core males at the Tirol Lek in 1976 were present throughout 1977. A fourth died in 1976, and the other two disappeared in 1977. Of four core males present in 1979, one died, one disappeared, and two occupied the lek in 1980.

2. Within the group a linear dominance hierarchy exists, individuals moving up in the framework with the loss of a superiorly placed member.

Table 4. Aggressive encounters among males at the Tirol Lek in 1976 and 1977. The number before the comma represents the encounters in which the dominant was victorious over the subordinate. The number following the comma represents the encounters in which the subordinate was ignored by the dominant individual with whom he had tried to initiate an aggressive interaction

Dominant	1976 Subordinate					
	KPK	OWO	GBK	GRW	PWR	GKW
KPK	–	2,	8,2			
OWO		–	7,	1,	1,	4,
GBK	1,		–			
GRW			1,	–		
PWR					–	
GKW						–

Dominant	1977 Subordinate				
	KPK	OWO	GRW	BWB	UFY
KPK	–	2,	12,2	9,1	2,1
OWO	2,	–	6,10	17,	
GRW	1,	3,	–	65,12	
BWB			6,1	–	
UFY					–

3. Position of dominance persists both within and between years as well as at different courts.

4. Dominance relates to right to display for the female and right to copulate (see below).

a) Aggressive Interactions. Position in the dominance hierarchy is determined by means of aggressive interactions among males that take place in the absence of females. Usually, these are performed on the display perch or adjacent perches by two or three birds. The aggression takes a number of forms (sometimes involving physical contact) including supplantings, chases, and vocal duels (Foster, unpubl. data). Also included are a series of ritualized displays strongly reminiscent of the Solo Precopulatory and Jump Displays of courtship. In the most common of these, the Fly-At Display, two males, facing each other or perched side by side perpendicular to the display branch, alternately fly up and (turning if necessary) directly at the other bird. The male hovers briefly in front of and slightly above his adversary with rapidly beating wings. He then returns to his perch while the second bird performs a similar routine. Jumps are accompanied by the *buzzee* call, and the sequence also ends with one bird giving the high pitched final call while the other cowers on the perch.

For 177 aggressive interactions involving the eight individuals at the Tirol Lek in 1976–1977, the outcome was unequivocal. The number of aggressive interactions in which a male is involved varies markedly according to his status in the hierarchy and the length of the hierarchy. Usually, only the birds toward the top and middle are consistently active, the latter being somewhat more active than the former (Table 4). Within this group, generally, the higher a bird's position, the fewer the interactions in which he engages. This is true for two reasons. First, the alpha and beta individuals generally initiate fewer challenges than the birds immediately below them. This is in contrast to other species with dominance hierarchies (e.g. Woolfenden and Fitzpatrick 1977). Secondly, though subordinates challenge any individual above them, they more frequently challenge the individuals nearest them in the hierarchy.

The aggressive encounters among the males at the Tirol Lek for 1976 and 1977 are summarized in Table 4. Despite the variation in numbers of interactions, the status of any particular male was rarely in doubt. In only 15 (of 177) instances did one bird successfully challenge (or in one instance ignore the challenge of) another higher in the hierarchy. Seven of these involved BWB dominating GRW, the male immediately above him, who, in turn, dominated or ignored BWB on 77 occasions. The other eight challenges involved three subordinate and three dominant individuals. However, it is not clear that subordinates who successfully challenged higher-ranking individuals really were dominating them. 'Victory' usually was assigned when the higher ranking individual was supplanted. Sometimes this appeared to be more an expression of the latter's reluctance to engage in aggressive behavior than of his submission. In 29 instances when a subordinate challenged a higher-ranking individual, attempting to supplant him or chase him from a perch, the latter simply ignored him rather than responding in either an aggressive or submissive fashion.

In an additional seven aggressive encounters observed at the Tirol Lek in 1978, one bird, BWR, dominated a second, USV, six times and ignored his challenge once.

b) Dominance. The rank of at least the alpha male is, perhaps, even more clearly defined on the basis of behavior other than that involving aggressive encounters. The alpha male is the only one who behaves as a sentinel and gives the repeated advertising calls at the primary court though other individuals may call antiphonally with him, or, on occasion, in a similar but softer and less persistent fashion by themselves. As sentinel, the dominant individual usually occupies a call perch 3–12 m above the group while subordinates spend most of their time near the display branch on perches 1–3 m high. The dominance of the sentinel individual is indicated also by the slowness with which subordinate males replace him. Dominant males were removed from the Tirol Lek on four occasions and from the Becker Lek once. In no instance did the beta male (or any other) attempt to assume the sentinel role until at least two days had elapsed. At this point, he engaged in tentative bouts of advertising from high perches in the area, but calling occurred at a relatively low rate, and the calls were considerably softer than those of the previously dominant individual. Call rate and loudness gradually increased as did length of the calling bouts, and by 5–6 days after the removal of the alpha male, the beta male had taken his place.

Dominance determined on the basis of male-male aggressive encounters paralleled the right to display and copulate. During 17 Jump Display bouts, I also observed non-displaying males perched in the immediate vicinity of the display branch. In all instances, the nonparticipating males were lower in the hierarchy than the dancing ones. On 13 occasions, the former made no attempt to join in the display. In four instances, they attempted to join but immediately were chased away (once) by the dancing birds or were repeatedly chased but returned and ultimately disrupted the entire sequence (3 times). Precopulatory display always was initiated by the highest ranking male present. A beta male initiated display in the absence of the alpha male at Court IV twice. This occurred two and three days after the dominant individual, KPK, was netted and laparotomized. He was injured in the net and was absent from the court for a few days after. Likewise, when a display sequence was interrupted, it always was reinitiated by the dominant male. With rare exception, the final call of the jump sequence was given by the dominant who in turn performed the Solo Display, always watched by the male(s) displaced as well as by any other males in the vicinity. Only once did another bird attempt to participate in the display (a beta male), and he immediately was chased from the site by the dominant.

Dominance is even more striking when copulation is considered. During a copulation bout, the male copulates with the female 1–6 times, alternating with additional Solo Display. Once, two females were present at the Tirol Lek at the same time. Following the Jump Display, KPK executed the Solo Precopulatory Display and ultimately copulated with both females. At least two other males watched but made no attempt to participate.

Because I saw relatively few copulation bouts, I also determined the number of times a particular male was responsible for the Solo Precopulatory Display in those instances in which copulation did not occur. Or, in the absence of both copulation and Solo Display, I determined the number of Jump Display bouts in which a male gave the final call. This gave a total of 33 observations (10 copulation bouts, 11 Solo Precopulatory Displays, and 12 final calls). A single individual, KPK, who was dominant on the Tirol Lek in 1976 and until his removal in 1977, was responsible for 18 of these (7, 5, and 6, respectively). On 17 December 1977, I removed him from the lek to determine who would assume dominance in his place. His position was taken by the beta male, OWO. He was responsible for one copulation bout, three Solo Precopulatory Displays (one performed before KPK was removed, but from which he was displaced immediately on KPK's return), and six final calls. After I was sure of OWO's dominance, I removed him from the lek. Dominance then passed to GRW, the gamma male under KPK and the beta male under OWO. GRW assumed the role of sentinel male and was dominant in all subsequent aggressive encounters. However, no females visited the lek during his tenure, and so no reproductive behavior was observed. One of the remaining copulation bouts and one Solo Display were performed by an unbanded male during the first week of my arrival in 1976. It is likely that the bird was KPK. The remaining copulation was performed by the dominant individual in 1979. The other instances of Solo Display can be attributed to two subordinate males who performed in the absence of the alpha male.

It may be argued that in addition to exciting the female for copulation, the Jump Display functions aggressively, ultimately determining which male copulates with the female. Although this display has an aggressive element to it, I believe that the right to copulate is tied to the alpha status already determined unequivocally on the basis of male-male encounters in the absence of the female. One would expect, therefore, that the use of the Jump Display in the presence of the female solely to determine copulatory dominance would be selected against, as it should delay copulation unnecessarily. The female's interest could be redirected, or she could be scared off or, perhaps, susceptible to stolen copulations by another male, as may occur in the Buff-breasted Sandpiper, *Tryngites subruficollis*, (Myers et al. pers. comm.). To analogize, one would expect the dominant male to, 'strike while the iron was hot.' Yet, it is he who always initiates, or, following interruption, reinitiates the Precopulatory Display. On one occasion, even, KPK and GBK had been engaged in a 5 min aggressive interaction when a female arrived at the court. Although the dominance of KPK already had been amply demonstrated, the two males immediately began a Jump Display before her, presumably for its excitatory effect. Likewise, on two occasions, when a subordinate tried either to reinitiate the Jump Display or to join in the performance of the Solo Display following a Jump Display, the dominant chased him from the site and then returned to his own display. Finally, four times a subordinate male tried to join a Jump Display already in progress and was chased away by a participating male. In all these instances, performance of the Jump Display for the determination of dominance was unnecessary.

c) Subadult and First-Year Males. As with the Long-tailed Manakins (Foster, unpubl. data), acquisition of the definitive male plumage in the Swallow-tail occurs gradually, requiring from 2–3 years. In contrast to the former species (Foster 1977), however, males may associate with a lek the year following hatching, i.e., when they are ca. one year old. One or more males in this stage was consistently associated with the Tirol Lek in 1976, 1979, and 1980, and in 1977, one visited regularly. Others were observed there occasionally in 1978. The persistence of the association is unclear. The first-year male marked in 1976 was not seen in subsequent years, and the first-year bird of 1977 was unbanded. However, the first-year male present in 1979 became the subadult consistently present in 1980. First-year males were active participants in Fly-At Displays and other aggressive interactions with males at the various display sites though they only occasionally visited the favored court. I did not observe their participation in any precopulatory displays. This is not unexpected as they were at the bottom of the dominance hierarchy.

Sick stated (1942, 1959a, b, 1967) that young males sometimes assume the role of the female during precopulatory displays performed by adult males. He noted that, "In this case uncoordinated jumps are often substituted for the hovering display-flight" (Sick 1967, p 17). I never saw this and suspect that instead of a Jump Display he was observing aggressive male-male Fly-At Displays at which the young males were spectators rather than participants. I have observed this several times, but the behavior of the young males is distinct from that of females, and the adult males do not direct their activities to the young males but largely ignore them.

Sick further states (1967, p 17) that in the second year the subadult male is green like the female, but with a red crown. In fact, females also may have a red crown, though it occurs less frequently and is less extensive in this sex (Foster, unpubl. data). However, birds cannot always be sexed accurately by crown color. Thus, it is likely that the 'young males' that Sick observed behaving like females were, indeed, females.

Males in subadult plumage also were regularly associated with the three leks. One each was present at the Becker and Swamp Leks in 1977, and one or two at the Tirol Lek in 1977–1980. These birds participated in all displays including precopulatory ones. Position in the dominance hierarchy appears to be related to age, the youngest birds having the lowest status. However, this may be an indirect relationship reflecting the correlation between position and length of association with the lek. Prior occupancy does seem to confer an advantage in terms of dominance. One male in advanced subadult plumage was dominant over two males in adult plumage who joined his lek after the individual to whom he was subordinate was removed. Interestingly, the testes may develop to full breeding size as early as the first breeding season following hatching; a cloacal protuberance also is present. Average testes volumes of 11 males in adult plumage, five in subadult plumage, and four in first-year plumage were, respectively, 56.7 mm^2 (range = 44.9–68.9), 52.4 mm^2 (range = 23.6–91.6), and 36.8 mm^2 (range = 10.5–50.3).

Discussion

1. Evolution of the Mating System

Probably the most common type of mating system among birds is resource-based monogamy in which males, dispersed through the habitat, display independently to attract females who choose among them on the basis of both the resources they offer and their genetic characteristics. The mating system of the Swallow-tailed Manakin differs from this in almost every respect, being a type of non-resource based polygyny in which males aggregate at traditional sites to perform communal displays and females choose mates on the basis of their genetic quality alone.

Two factors generally preadapt species for a polygynous/genetic choice system. One is the emancipation of the male from parental duties (Lack 1968). The other factor is the inability of males to control access by females to resources required for breeding or to control the access of other males to areas where females are numerous for whatever reason [harem defense polygyny (Emlen and Oring 1977; Borgia 1979)]. Because the male offers no material benefits to the female either before copulation or during the rearing of young, she chooses a mate on the basis of his genetic quality alone.

As far as is known, female Swallow-tails do not congregate in any particular area, and, thus, access cannot be controlled in this manner. Likewise, male Swallow-tails contribute nothing to the reproductive effort except sperm. In addition, nest sites of this manakin are non-specific and ubiquitous and, therefore, unmonopolizable. This also is true of the food supply. Though these manakins exploit a wide variety of foods during the breeeding season, fruits, patchily distributed through the forest on large, heavily laden trees, are a major component. At any one time, these trees contain a supply in excess of that required by many manakins and are so large, that control would be extremely costly, if not impossible, and, therefore, of no benefit to the males. Bradbury (1981) has suggested that under such circumstances, males will switch from a system that emphasizes resource monopoly to one that involves 100% self-advertisement.

The shift to a system of self-advertisement is independent of the dispersion pattern exhibited by the males. Males of some species may continue to be evenly spread through the habitat, whereas others aggregate at traditional sites such as leks or arenas. Numerous attempts have been made to explain why males of some species aggregate while others do not. A variety of advantages associated with group living have been outlined by Emlen (1978; see also Stallcup and Woolfenden 1978). However, these generally are not considered sufficiently compelling to have caused and to maintain the existence of male clusters (Alexander 1975; Bradbury 1981). Bradbury (1981) argues that aggregation is of no benefit to the male and may, in fact, be to his detriment. Rather, male groupings may be maintained because they are advantageous to females who, thus, visit them in preference to solitary males (Alexander 1975; Bradbury 1981). As a result, the reproductive success of males in groups averages higher than that of solitary males. Potential benefits to females are of three types. First, because males are gathered in one or a few areas where all copulations occur, females, particularly young ones lacking experience in 'evaluating males,' can monitor the mate choice of other females. This is not likely to be important to Swallow-tailed Manakins as multiple females are present at a lek only very rarely.

A second advantage derives from the use of traditional sites; females know their location and can visit them at any time with a high probability of finding several sexually active males. Female *C. caudata* definitely are aware of the location of the various courts. On three occasions a female visited a court when no sentinel or other males were present or calling. In each instance, the females flew directly to the display perch, wingflicked, jumped up and down, and peered all around the vegetation making soft calls before departing.

The third and most obvious advantage of the male cluster is the opportunity it provides for females to compare multiple males rapidly, simultaneously, with relatively little effort, and at a place away from the nest site. This decreases the probability of nest location by predators (Alexander 1975). It also, presumably, facilitates female choice. Whether or not this benefit applies to *C. caudata* females is not clear. In classical lek species (e.g. Lill 1974b, 1976; Pitelka et al. 1974; Wiley 1974), each court is occupied by only one male and represents his defended territory. Males display simultaneously, but independently, and female choice among them is unrestricted, a requirement for lek behavior according to current definitions (Borgia 1979; Bradbury 1981). In the Swallow-tailed Manakin, in contrast, though two (or occasionally three) males display at one time, the female, in fact, does not choose among them. Rather, positions of the males in the dominance hierarchy determine who copulates with the female at a particular arena; in practice, the dominant male controls her access to the other males *not* by controlling her, as in a system of harem defense polygyny (Emlen and Oring 1977; Borgia 1979), but by controlling the other males and preventing them from displaying (Solo Precopulatory Display) for her. Borgia (1979) considered this something of a 'non-argument,' suggesting that if a subordinate's characteristics were such that females preferred him to the dominant, then the high quality male would leave the lek and display independently, and females would seek him out. The situation probably is not so simple, as solitary males would be less apt to be contacted by large numbers of females if groups of males also were available (see arguments in Bradbury 1981).

Another influencing factor is how a female assesses the genetic characteristics of the males involved. Though this is not known, a number of possibilities, inapplicable to solitary males, exist. The most common is assessment based on male status as determined by the placement of his territory on an arena or his position in a dominance hierarchy, either of which supposedly is indicative of his prowess relative to other males. Alternatively, females may examine male-male interactions, themselves, rather than just their outcomes in terms of status. Although female *C. caudata* may not be able to choose among the males in a group, they may visit, compare, and choose among groups at different leks. The strength of the dominance exerted by the alpha male over his subordinates would be the critical factor. Borgia (1979) suggested that females should not mate with males repeatedly disrupted during courtship but should abandon such leks in favor of one at which the male is more secure in his position. This may be what happens at *C. caudata* leks when females leave without copulating after the displays are repeatedly interrupted. Disruption may occur more frequently in the Swallow-tail than in non-cooperative lek species, because males are so closely associated as a group rather than each being concerned only with occupying and defending his own territory. If cooperative displays represent a cost/benefit trade-off which increases the probability of copulation by increasing female stimulation, but, at the same time, decreases the probability of copulation by increasing the chance of disruption, then, when the costs of the latter outweigh the benefits of the former, one may expect to find exploded leks as in *C. linearis* (Foster 1977).

It also may be that females do not distinguish between the top several males in a dominance hierarchy but, in fact, are willing to accept mating with (and thus 'choose') the dominant male present at the lek *at the time of the visit* as long as he occupies some minimum position. On two occasions, a subordinate male performed the Solo Precopulatory Display for a female in the absence of the alpha male. Both times, the latter arrived and disrupted the sequence. Though copulation did not occur, the female appeared to be receptive and gave the impression that she would have copulated with the subordinate had he not been displaced.

If females choose mates on the basis of their demonstrated dominance or fighting ability, one can see the selective advantage of the substitution of a ritualistic sequence for real combat. It should minimize the expenditure of time and energy on the parts of both combatants as well as decrease the likelihood that either one will sustain any lasting injury. Along with the advent of the dominance hierarchy, it may also minimize display disruption. [But, disruption does occur in non-cooperative, territorial lek species, as well (e.g. Hamerstrom and Hamerstrom 1960; Kruijt and Hogan 1967; Lill 1974a, 1976; Myers et al., pers. comm.).] The Jump Display of the Swallow-tailed Manakin does seem to serve these functions and to increase the probability that copulation will occur. It, thus, is a critical element in courtship (as suggested above), not merely a determinant of dominance, and participation by the subordinate contributes to the fitness of the dominant.

Though male-male interactions apparently benefit the dominant male and the female, advantages accruing to the subordinate as a result of his participation are more difficult to identify. As long as the outcome of any interaction is not predetermined, then a male should always participate in an aggressive encounter, as the possibility always exists that he may win. In the Swallow-tailed Manakin, however, the Jump Display is not aggressive but serves to attract and excite females for copulation. Its outcome is not in question but is determined by the males' positions in the dominance hierarchy defined by male-male interactions in the absence of the female. Given this, there must be a point at which the probability of the subordinate dancer copulating is so low that the possibility of benefit accruing is outweighed by the cost of the dance in time, energy, or increased exposure to predators, etc. If the probability is low enough, and a subordinate can accurately assess in advance that he will lose the encounter, as seems to be the case here, then selection should favor those subordinates who do not perform the Jump Display. Why then, do the subordinates dance?

It is not necessary to invoke altruism in order to explain this behavior, as no reason exists to suspect that the fitness of the subordinate decreases as a consequence of his participation. In fact, fitness may be enhanced. This requires only that his overall fitness be greater than that of a nondisplaying group member. Direct comparison of the success of these types is not possible as the latter does not exist. However, it does appear that an increased fitness of cooperatively displaying males could be achieved in several ways. First, the opportunity for stolen copulations exists even if they only rarely occur. Certainly, subordinate dancers are more likely to steal copulations than are non-dancing males if only because females may be more apt to be receptive to males that exhibit some level of aggressive interaction. It also may be that proper execution of the displays requires a certain amount of experience, which a male acquires by dancing as a subordinate. This could influence eventual reproductive success as well as the ability of a male to maintain or improve his position in the dominance hierarchy. Subordinate males attentively observe the dominant while he performs the Solo Precopulatory Display and copulates, and males low in the hierarchy engage in 'practice displays' (both reproductive and aggressive) by themselves.

Delayed benefit might also arise if females exhibit any 'lek faithfulness' whose strength is influenced by the outcome of previous visits to the lek. If so, then by participating in the Jump Display and enhancing the experience of a female on a particular visit, a subordinate may increase the probability that the female will return to the lek for subsequent matings. This would be to his benefit if he is likely to become dominant at the lek in the future, as seems likely. A subordinate should outlive those birds above him in the dominance hierarchy, since the more highly placed birds generally are older. The dominant individual, in addition, acting as sentinel, may be more conspicuous to predators. With the loss of any bird, all subordinate to him move up a step in the hierarchy. Thus, if a male can live long enough, he eventually will acquire dominance on a lek of his own. A similar type of delayed benefit is suggested for wild turkeys (Watts and Stokes 1971).

The subordinate males also could benefit from the cooperative behavior through kin selection. If males occupying a lek are closely related, then subordinate males may be able to increase their inclusive fitnesses even in the absence of copulation. At present, data on the relatedness of males in a group are not available. However, this represents an important area for future study.

Finally, it is possible that the system is self-generating/sustaining simply as the result of female preference. We can assume that in the ancestral form from which the Swallow-tail was derived, males aggregated at arenas for simultaneous, but independent displays, as is characteristic of most lek systems. Certain males, presumably, engaged in aggressive interactions in which they repeatedly challenged or displaced one another. Females were preferentially attracted to such interacting males, and the aggressive encounters became ritualized in the behavioral repertoire of the species as the Jump Display. If certain males were more aggressive than others and showed a greater propensity for this type of interaction, and if this propensity were at least partially controlled genetically, then such genes would spread through and become fixed in the population. As long as females favored males interacting in this manner, the behavior would be maintained.

Acknowledgements. I am particularly indebted to Ing. Hernando Bertoni, Minister of Agriculture of Paraguay, Col. C.R. Wallace, US Embassy, Asunción, Lee and Nicki Donnell, Phil and Peg Myers, Roger Myers, Armando and Miguela Reynaers, Erik Reynaers, and Jim and Nancy Talbot who greatly facilitated my work in Paraguay. J.P. Myers, K.W. Corbin, H.W. Greene, and F.A. Pitelka read an early draft of the manuscript and offered some extremely helpful comments. R.E. Jones provided some field assistance, and R.W. McDiarmid, G.F. Barrowclough, R. Diez, Sr. and Sra. Hugo Beckers, M.K. LeCroy, P. Myers III, M. Walter, and R.M. Wetzel contributed in other ways. The study was supported by Grant No. 7699 from the Penrose Fund of the American Philosophical Society, a grant from the National Geographic Society, and funds from the Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, and the Department of Biology, University of South Florida, Tampa. To all of these individuals and institutions I extend my sincerest thanks.

References

Aldrich JW, Bole BP Jr (1937) The birds and mammals of the western slope of the Azuero Peninsula. Cleveland Mus Nat Hist Sci Publ 7:1–196

Alexander RD (1975) Natural selection and specialized chorusing behavior in acoustical insects. In: Pimentel D (ed) Insects, science and society. Academic Press, New York, pp 35–77

Borgia G (1979) Sexual selection and the evolution of mating systems. In: Blum MS, Blum NA (eds) Sexual selection and reproductive competition in insects. Academic Press, New York, pp 19–80

Brown JL (1978) Avian communal breeding systems. Ann Rev Ecol Sys 9:123–255

Bradbury JW (1981) The evolution of leks. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior. Chiron Press, New York, pp 138–169

Emlen ST (1978) The evolution of cooperative breeding in birds. In: Krebs JR, Davies NB (eds) Behavioural ecology an evolutionary approach. Sinauer, Sunderland, MA, pp 245–281

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Foster MS (1977) Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. Am Nat 111:845–853

Friedmann H, Smith FD (1955) A further contribution to the ornithology of northeastern Venezuela. Proc USNM 104:463–524

Gilliard ET (1959) Notes on the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). Am Mus Nov no 1942

Gilliard ET (1963) The evolution of bowerbirds. Sci Am 209:38–46

Hamerstrom F, Hamerstrom F (1960) Comparability of some social displays of grouse. Proc XII Int Ornithol Cong, pp 274–293

Ihering R von (1936) El tangara o "bailarin" Chiroxiphia caudata. El Hornero 6:311–313

Kruijt JP, Hogan JA (1967) Social behavior on the lek in Black Grouse *Lyrurus tetrix tetrix* (L). Ardea 55:203–240

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Lill A (1974a) Sexual behavior of the lek-forming White-bearded Manakin (*Manacus manacus trinitatis* Hartert). Z Tierpsychol 36:1–36

Lill A (1974b) Social organization and space utilization in the lek-forming White-bearded Manakin, *M. manacus trinitatis* Hartert. Z Tierpsychol 36:513–530

Lill A (1976) Lek behavior in the Golden-headed Manakin *Pipra erythrocephala* in Trinidad (West Indies). Adv Ethol 18:1–84

Meyer de Schauensee R (1970) A guide to the birds of South America. Livingston, Wynnewood, PA

Olrog CC (1959) Las aves Argentinas una guia de campo. Inst Miguel Lillo, Tucuman, Argentina

Pitelka FA, Holmes RT, MacLean SF Jr (1974) Ecology and evolution of social organization in Arctic Sandpipers. Am Zool 14:185–204

Sick H (1942) Die Balz von *Chiroxiphia caudata*. Ornithol Monatsber 50:18

Sick H (1959a) Die Balz der Schmuckvogel (Pipridae). J Ornithol 100:269–302

Sick H (1959b) Estudo comparativo das cerimonias pre-nupciais de piprideos Brasileiros. Bol Mus Nac Nova Ser, Rio de Janeiro, Brasil Zool 213:1–17

Sick H (1967) Courtship behavior in the manakins (Pipridae): a review. Living Bird 6:5–22

Skutch AF (1935) Helpers at the nest. Auk 52:257–273

Skutch AF (1961) Helpers among birds. Condor 63:198–226

Snow DW (1963) The display of the Blue-backed Manakin, *Chiroxiphia pareola*, in Tobago, WI. Zoologica 48:167–176

Snow DW (1976) The web of adaptation bird studies in the American tropics. Quadrangle/NY Times Book Co, New York

Sokal RR, Rohlf FJ (1969) Biometry. Freeman, San Francisco, CA

Stallcup JA, Woolfenden GE (1978) Family status and contributions to breeding by Florida Scrub Jays. Anim Behav 26:1144–1156

Vigil C (1973) Aves Argentinas u Sudamericanas. Editorial Atlantida, Buenos Aires

Watts CR, Stokes AW (1971) The social order of turkeys. Sci Am 224:112–118

Wetmore A (1972) The birds of the republic of Panama. Pt 3. Smithsonian Inst Press, Washington, DC

Wiley RH (1973) Territoriality and non-random mating in Sage Grouse *Centrocercus urophasinus*. Anim Behav Monogr 6

Wiley RH (1974) Evolution of social organization and life history patterns among grouse. Q Rev Biol 49:201–227

Woolfenden GE, Fitzpatrick JW (1977) Dominance in the Florida Scrub Jay. Condor 79:1–12