THE CONDOR
A JOURNAL OF AVIAN BIOLOGY

Volume 95 Number 4 November 1993

The Condor 95:769–781

VOCAL REPERTOIRE OF THE LONG-TAILED MANAKIN AND ITS RELATION TO MALE-MALE COOPERATION[1]

JILL M. TRAINER
Department of Biology, University of Northern Iowa, Cedar Falls, IA 50614

DAVID B. MCDONALD
Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33852

Abstract. We examined the vocal repertoire of lek-mating Long-tailed Manakins (*Chiroxiphia linearis,* Pipridae) in Monteverde, Costa Rica. Males in this genus are unusual in performing a cooperative courtship display, including duet songs and coordinated dual-male dance displays. Males give at least 13 distinct vocalizations, several of which occur in clear behavioral contexts. By observing the behavioral context and the sequence in which calls were given, we found that the most frequent calls occurred during three types of activity: song bouts, dance, and noncourtship interactions. The responses of males to playback of six vocalizations indicated that the calls function as much in mediating cooperative interactions as in expressing male-male agonism. The evolution of the large vocal repertoire in Long-tailed Manakins may be associated with their unique social system based on long-term, cooperative relationships among males.

Key words: Vocalization; call function; Long-tailed Manakin; Chiroxiphia linearis; *sociality; cooperation, lek.*

Resumen. Estudiamos el repertorio vocal del Saltarín Toledo (*Chiroxiphia linearis,* Pipridae) en Monteverde, Costa Rica. Los machos de este género se comportan muy particulares en relación el cortejo cooperativo, incluyendo canciones a duo y danzas coordinadas de parejas de machos. Los machos emiten al menos 13 vocalizaciones distintas, muchas de ellas con un contexto claro con respeto al comportamiento. Se encontró, mediante observación del contexto de comportamiento y las secuencias de sus vocalizaciones, que las llamadas más frecuentes se emiten durante tres tipos de actividades: el canto, el baile, y la interacción no-relacionada al cortejo. Las respuestas de los machos a seis vocalizaciones pre-grabadas sugieren una función de interacción cooperativa tanto como para expresar agresión entre machos. La evolución de las vocalizaciones diversas en *Chiroxiphia linearis* puede ser asociada con el sistema social unico fundado en relaciones cooperativas a largo plazo entre machos.

INTRODUCTION

Although much information exists on the use and function of vocalizations in territorial songbirds, little such information exists about passerines with other social systems. Here we describe the diverse vocal repertoire of a lek-mating species, the Long-tailed Manakin (*Chiroxiphia linearis*). Lek social systems differ from those of most passerines in that males provide no resources valuable to breeding females other than gametes (Bradbury 1981). In addition, lek species lack persistent pairbonds and do not defend exclusive, resource-based territories. Long-tailed Manakins are especially unusual in that groups of males form complex networks of cooperative alliances (McDonald 1989a). This cooperation involves a joint courtship display that consists of highly coordinated singing and dancing performed by two males (Snow 1977, Foster 1981,

---

[1] Received 11 March 1993. Accepted 8 July 1993.

McDonald 1989b). Our results suggest that the functions of Long-tailed Manakin calls reflect the importance of cooperative as well as aggressive interactions among males, in contrast to what is observed in territorial species.

Chiroxiphia manakins are unusual among their suboscine relatives in possessing a large and varied repertoire of vocalizations. Several species of manakins have mechanical pops and snaps in the acoustic repertoires, but generally, manakin vocalizations are few in number and simple in structure (Prum 1990b). The Long-tailed Manakin's repertoire of 13 distinct calls is rich, even when compared to the call repertoires of songbirds (exclusive of primary song variants). A major factor contributing to the evolution of such a diverse repertoire may be the complex network of long-term relationships among males.

Here we describe the functions of Long-tailed Manakin vocalizations, and examine the complexity of the vocal repertoire in the context of sexual selection and the social structure. We employed three approaches in our study. (1) We observed the social and behavioral context of each call. (2) We analyzed the sequence in which calls were given. These approaches allowed us to identify three general contexts in which the majority of calls occurred. (3) We recorded the responses of manakins to experimental playback of taped calls in the field.

NATURAL HISTORY AND DISPLAY

A Long-tailed Manakin lek consists of a core partnership of an alpha and a beta male and as many as 11 male affiliates (McDonald 1989b). These males regularly attend a traditional display area called a perch-zone or lek arena, which contains one or two major perches for the dance display. Perch-zones are separated by 75–300 m, and each is occupied by a different alpha male. From a particular perch-zone, one can sometimes hear the singing of manakins in other zones, but cannot see them.

Plumage maturation occurs over a four-year period with distinct, age-specific, predefinitive stages (McDonald 1989b, 1993a). Affiliates of a perch-zone may include both definitive and predefinitive males. Affiliations among males develop over their lifetimes of at least 13 years (McDonald 1993b) and result in the establishment of a dominance hierarchy. The alpha male is highest ranking, and with very rare exceptions only he mates with female visitors. Pairs of displaying males tolerate the presence of other affiliates, and overt aggression among males is rare.

In order to attract females to the perch-zone, two male partners cooperate in performing the coordinated song and dance displays. The courtship display usually is performed by the alpha and beta, although occasionally other combinations of affiliates may display (McDonald 1989b). Males begin by broadcasting long bouts of unison duet song, or *toledos,* from the lower branches of a tree crown (subcanopy). If a female arrives, both males and the female descend to the dance perch, a horizontal branch or vine within 1.5 m of the ground. The males begin a series of 20–100 backward leapfrog hops alternating with as much as 60 sec of a special *butterfly flight* characterized by deep wing beats. A dance bout may include as many as 10 sets of hops and *butterfly flight.* Dances leading to copulation include a solo *butterfly flight* by the alpha male. At times, two or more males, often including predefinitive males, gather on a dance perch in the absence of a female and perform a variation of the hops (*popcorns*), in which males jump straight up and do not leapfrog over the partner(s).

METHODS

The study area, in Monteverde, Costa Rica (10°18′N, 84°48′W), is 80 ha of premontane tropical moist forest (Holdridge 1966) at an elevation of 1,300 m. McDonald uniquely color-banded 270 manakins between 1981 and 1987. The sex of individuals with green plumage was determined by subsequent observations of behavior.

Vocalizations were recorded with a Sony WM D6C cassette recorder and a Sennheiser ME 80 directional microphone. In addition, behavior sequences were recorded in the field using a Tandy 102 personal computer programmed as an event recorder. Sonagrams were made using a Kay Elemetrics Model 5500 Sonagraph and grey scale printer. A synoptic tape of the Long-tailed Manakin vocal repertoire is on file at the Library of Natural Sounds at the Cornell Laboratory of Ornithology (Accession #49097).

The terms "call" and "vocalization" are used interchangeably to denote an individual utterance of sound. "Song" refers only to the *toledo* call, which is given in unison as a duet by singing partners. "Call type" refers to one of the 13 acoustically distinguishable kinds of manakin calls. The term "dance bout" refers to a display sequence including one or more of the following elements: a variable number of sets of leapfrog dance hops, dual-male *butterfly* display, and solo display by the alpha male. A "dance bout" is, therefore, essentially synonymous with a single continuous visit to the dance perch by one or more females, because males almost invariably display throughout female visits.

BEHAVIORAL CONTEXT

Ad libitum observations of vocal behavior and responses of male and female manakins were made at perch-zones. In addition, observers conducted scheduled two-hour observations from blinds 8–12 m from display perches between 06:00–15:00. During the scheduled observation periods, an observer recorded the number of *toledo* and *teeamoo* calls occurring in each 5-min block, and the number of female and male manakins present in the perch-zone during the first min of each 5-min block. The details of this behavioral sampling protocol were described in McDonald (1989a).

SEQUENCE ANALYSIS

Thirty real-time samples of vocalizations were recorded on cassette tapes. The samples were of different durations and together totaled 285 min. The transitions between calls were transcribed in the sequence heard, regardless of the identities of the callers. Thus, transitions represented the call sequence of all males together rather than of individuals. Two vocalizations separated by more than 30 sec were not scored as a transition.

We tested whether the occurrence of a given call type depended on the immediately preceding type using chi-square contingency analysis as described in Trainer (1988). Transitions among the seven most frequent call types were analyzed, excluding those calls normally given on the dance perch. Four infrequent calls (*doodoodoo, toodleloo, chitter,* and *squawk*) were excluded because sample sizes were insufficient for chi-square analysis.

Because we were interested in how different call types were arranged in sequence, our analysis concerned only those transitions between unlike call types. Like many birds, Long-tailed Manakins tend to repeat most calls several times before switching to a different call type. Such call repetitions are extremely numerous and eclipse the importance of transitions between unlike call types in a contingency analysis (Lemon and Chatfield 1971). Therefore we excluded transitions between identical call types when calculating the expected values. Expected values were calculated by iteration (Goodman 1968, Trainer 1988) because simply using row and column totals is not valid for an incomplete matrix.

Comparing the observed and expected frequencies of each call type transition revealed those pairs of call types that tended to occur or not to occur together in sequence. To obtain a consistent criterion for identifying major departures from expected values, we collapsed the contingency table around each matrix cell, combining frequencies from other call types to form 42 two-by-two matrices (Slater 1973). We tested the resulting chi-square values at the 0.05 level. The chi-square analyses of the two-by-two matrices were not intended as significance tests; rather, they indicate those transitions that contribute most to the nonrandom sequence of call types overall.

PLAYBACK EXPERIMENT

The vocal responses to each of five manakin call types were tested by broadcasting recorded calls through an Aiwa SC-A2 speaker. Each test consisted of broadcasting one type of call and writing down all vocalizations heard during a playback period. The frequencies of occurrence of response vocalizations were compared to their baseline frequencies during a preplayback period in which nothing was broadcast. All calls except *toledos* were broadcast from the ground near the dance perch. For these calls, *nyanyownh, teeamoo, weet,* and *wheeoo,* a five-minute preplayback period was followed immediately by 5 min of playback at the rate of 1 call/min. *Toledo* songs were broadcast from a speaker suspended from a tree 6 m above the ground at a rate of 24 songs/min. For the *toledos,* the duration of the preplayback and playback periods were each 10 min. At a given perch, we tested three different call types on the same day with 10 min between experiments. Each type of call was broadcast at 10 different perches. For each of the six most frequent vocal responses, the numbers of calls during the preplayback and playback periods were compared using one-tailed Wilcoxon matched-pairs signed-rank tests. Because this resulted in 26 simultaneous tests, we used a sequential Bonferroni technique (Rice 1989) to adjust the significance level. Individual comparisons were considered significantly different if $P \leq 0.002$,

TABLE 1. Descriptions and uses of Long-tailed Manakin call types. The quantities in parentheses are the number of occurrences of the call in the recorded samples.

Call	Call recipient	Amplitude	Frequency of occurrence	Function of call
During-song-bout				
toledo	female	loud	abundant (1119)	Attract females
wit	partner, female	soft	abundant (751)	Synchronize singing of partners, precedes social interaction with affiliate or female
owng	partner, female	soft	infrequent (42)	Stimulate female to move to dance perch
Dance				
nyanyownh	female	loud	abundant	Accompany courtship dance display
buzz-weent	subordinate partner	loud	infrequent	Signal dominance
Noncourtship				
teeamoo	partner	loud	intermittent (294)	Attract partner
weet	male	loud	intermittent (143)	Mild distress
Other				
waanh	male	soft	intermittent (418)	Close proximity contact call
doodoodoo	male	soft	infrequent (13)	Uncertain
toodleloo	male	soft	infrequent (12)	Uncertain
wheeoo	strange male, predator	loud	intermittent (114)	Mobbing call
chitter	dominant male	soft	infrequent (4)	Signal submissiveness
squawk	predator	loud	infrequent	Distress in mist net

yielding a maximum, simultaneous significance level of 5%.

RESULTS

BEHAVIORAL CONTEXT

Most of the call types (Table 1) were given exclusively by male manakins. Rarely, banded females were observed to give *wheeoo* calls as described below. Both sexes gave the mist net distress call, *squawk,* although females were more likely to vocalize than males. The names of the calls were intended to be onomatopoeic.

Toledo—a loud song, almost always sung as a duet by two males perched approximately 10 cm apart on a branch (Fig. 1b). Usually the alpha and beta males sang together as partners, but sometimes other combinations of males affiliated with a perch-zone performed the duet. The song contribution of each male consisted of a continuous loud, pure tone of alternately falling and rising pitch approximately 0.60 sec in duration. The two males' songs overlapped with one male beginning to sing approximately 0.10 sec after his partner. For a sample of 1,583 bouts of *toledos* by one set of partners the mean number of *toledo* songs per bout was 48.6 delivered at a rate of 15.6 songs/min. Manakins were extremely persistent singers; over entire seasons, mean *toledo* rates by the most active teams exceeded 300/hr (McDonald 1989a). During a single 2 hr scheduled observation period one pair delivered 1,919 songs. On a calm day *toledos* could be heard from a distance of up to 250 m.

Rarely, we heard a *toledo* sung by a single male, and these usually occurred during a bout of normal duet songs. No bout of more than eight consecutive solo *toledos* was noted during more than 3,000 hours of scheduled observation. Also infrequent were *toledos* performed by three males together and McDonald observed only two cases of four males calling together in synchrony. Manakins sang *toledos* from the forest subcanopy, usually from the lower branches of a tree crown, 5–15 m from the ground. The long, loud bouts of song appeared to attract females to the perch-zone (McDonald 1989a). When females approached the dance perch, males switched to dual-male dance displays on the perch.

An interesting feature of courtship display in this species is the lack of any diurnal pattern of activity in singing or dancing (McDonald 1989a). Many other species of lekking birds, including other species of manakins are noted for pronounced morning and afternoon peaks in activity

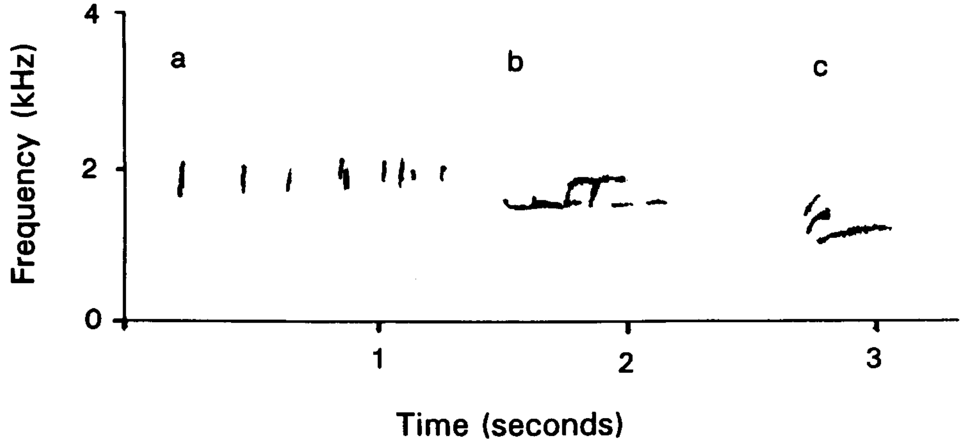

FIGURE 1. During-song-bout Vocalizations of Long-tailed Manakins. (a) *wits,* (b) *toledo,* (c) *owng.*

(e.g., Snow 1962, Lill 1976, Bradbury et al. 1989, Atwood et al. 1991).

Wit—a brief, soft note, 0.10 sec in duration (Fig. 1a). Partners alternated giving *wits* in a rapid series of 10–25 calls. *Wits* were usually delivered by two partners perched close together in the subcanopy immediately before beginning a bout of *toledos.* In addition, slower series of *wits* were associated with the *owng* call, and sometimes preceded dual-male display for a female, or occurred when a female was near the dance perch and only one high-ranking male was present at the perch-zone, as described further below for the *owng* call.

Owng—a brief, soft vocalization with an interrogative sounding quality given intermittently from the subcanopy (Fig. 1c). Often singing males interjected *owng* calls during bouts of *toledos.* Sometimes singing would become erratic, with frequent interruptions containing long bouts of *wits* and *owngs.* This erratic singing may have been associated with the arrival of a female that had not yet descended to the dance perch. Such females would not necessarily be visible to observers sitting in a blind, but observers sometimes recorded the appearance of a female on the dance perch after erratic song bouts. In addition to this context, a lone male would give bouts of *wits* and *owngs* when a female was near the dance perch, but no partner was present to perform the dual-male display. Such bouts of *wits* and *owngs* were often followed by solo *butterfly* display by the calling male.

Nyanyownh—a loud, nasal call given by both males on the dance perch (Fig. 2a). The *nyanyownh* accompanied each hop in the leapfrog portion of the dance display. A sample of 95 dance bouts that progressed from the dual to the solo stage contained a mean of 3.9 sets of leapfrog hops (range = 1–11, SD = 2.6) interspersed with dual-male *butterfly* displays. The mean number of leapfrogs per set was 34.8 (range = 2–139, SD = 12.0). The silent, dual-male *butterfly* displays lasted a mean of 26.3 sec (range = 2–75, SD = 12.2), during which males flew in radial flights within 5–20 m from the focus at the dance perch.

Buzz-weent—a loud call associated with the leapfrog portion of the dance display (Fig. 2b). After one or more series of leapfrog hops, the dominant male delivered *buzz-weent* from between the female and his partner, along the axis of the dance perch. He directed the call toward the partner, while facing away from the female. The male giving the call then left the perch while his partner remained on the perch with the female. Directed *buzz-weents* also occurred during dances in which several males but no females were present. *Buzz-weents* with no other males present were given by males of all ages.

In 20 of 129 dance bouts with suitable data between 1984 and 1988, the subordinate male left the perch area after *buzz-weents* that followed the final or final two sets of leapfrog hops. The dominant male then began solo *butterfly flight.* In 33 of the 129 dance bouts, however, three or more *buzz-weents* occurred without subsequent departure of the beta male. Furthermore, in 76 of the dance bouts, the lower-ranking male

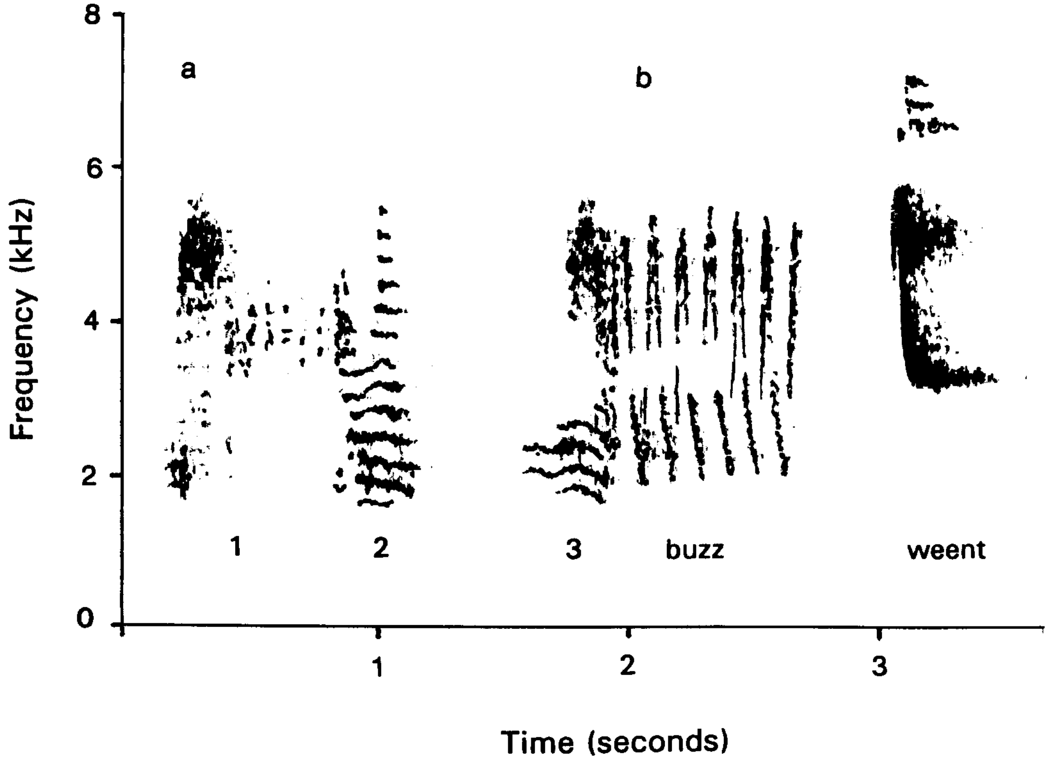

FIGURE 2. Dance Vocalizations. (a) three *nyanyownh* calls, (b) *buzz-weent.*

dropped out of the dual-male portion of the dance display without any *buzz-weent* calls being given. The *buzz-weent* call, therefore, was neither necessary nor sufficient to produce the transition from dual-male to solo male dance display.

Buzz-weents were given only when the dancers had disparate dominance ranks; males directed the call toward other males to whom they were clearly dominant, and definitive males directed calls toward predefinitive males. This call was not heard between males of nearly equal or equivocal dominance status. For 179 *buzz-weents* where both the caller and the recipient could be identified, in every case, the male who gave the *buzz-weent* was known, by other criteria, to be dominant. In 160 of the cases the male giving the call was an alpha male, and in 21 cases the call was given by a definitive male toward a predefinitive male.

Teeamoo—a loud call, approximately 1.0 sec in duration, consisting of two pure tones, the first descending in pitch to approximately the frequency of the second (Fig. 3b). *Teeamoos* were given intermittently at intervals of approximately 20 sec, usually by high-ranking males when no other high-ranking male was in the immediate vicinity. Of 182 *teeamoos* for which the identity of the caller was known, 139 (76%) were by the alpha male, while the beta was absent. Often following a *teeamoo* call, a partner would arrive, perch next to the caller, exchange *wit* calls and begin to duet with him. Data from the scheduled observation periods provided evidence that *teeamoos* were used to attract a partner to sing a *toledo* duet. Before *toledo* bouts, males tended to give *teeamoos* when they were alone in the perch-zone, and tended not to do so when their partners were already present ($G = 28.52$; $df = 1$; $P = 0.001$) (Table 2). Often a dance partner would *teeamoo* while the alpha male performed solo *butterfly flight* following a dual-male dance display for a female.

Weet—a brief, loud, sharp call given intermittently from the subcanopy (Fig. 2a). *Weet* calls were associated with situations involving mild distress. For example, males gave *weets* when a partner failed to respond to repeated *teeamoo* calls. *Weets* were sometimes given when a hu-

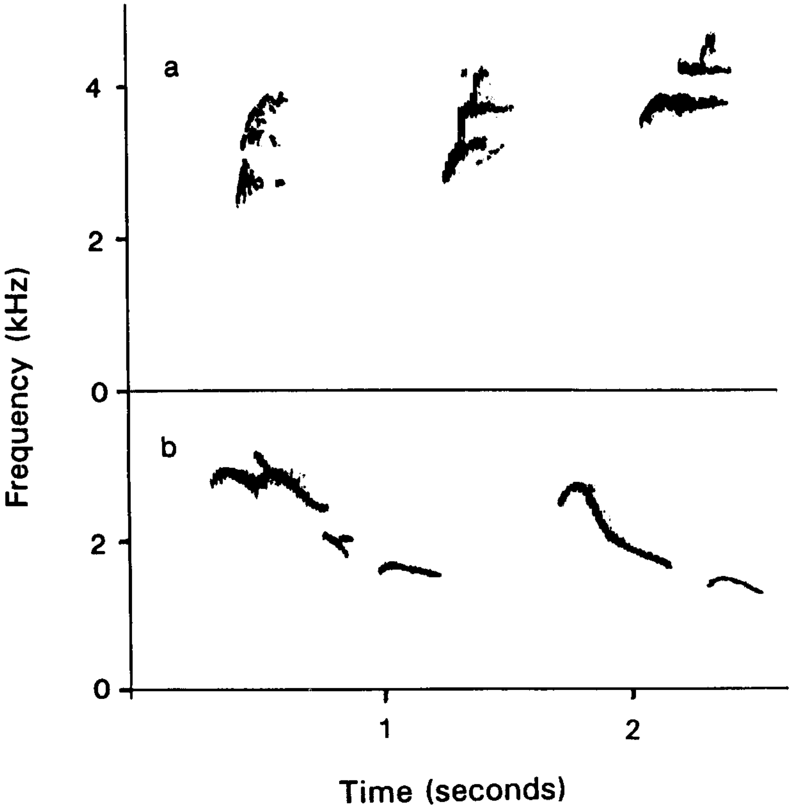

FIGURE 3. Noncourtship Vocalizations of Long-tailed Manakins. (a) three *weet* calls, (b) two *teeamoo* calls.

man observer disturbed a male manakin in the perch-zone.

Waanh—a soft, nasal, descending call given intermittently from the subcanopy (Fig. 4a). *Waanh* was used in a variety of situations, including during song bouts and during noncourtship interactions. Often *waanh* was given by males when they were neither singing nor dancing. For example, this call was given by assemblages of predefinitive males who were not displaying, or by a third definitive male in the presence of two displaying males.

Doodoodoo—a call consisting of three or four soft tones of the same pitch, given in the subcanopy (Fig. 4d). It was usually given by a male who was not engaged in singing or dancing. Because this call was given infrequently, a more specific context was not detected. Human imitation of the call often served to elicit close but silent approach of males.

Toodleloo, tuhweeko, federico and variants—a variety of calls consisting of soft tones of alternately falling and rising pitch, given infrequently in the subcanopy (e.g., the *toodleloo* of Fig. 4e). Like *doodoodoo,* these calls were usually given by males who were not engaged in singing or dancing, but a more specific context could not be ascertained. Many of the calls markedly resembled portions of the *toledo* or *teeamoo* calls but were never given in unison and were always of considerably lower amplitude.

TABLE 2. Number of song bouts preceded or not preceded by teeamoo calls when one or two males were present before the song bout.

	Song bouts preceded by teeamoo[a]	Song bouts not preceded by teeamoo
One male present[b]	41	9
Two males present[b]	15	35

[a] At least one teeamoo call occurred in the five-minute sample block preceding the start of the song bout.

[b] During the sample minute preceding the start of the song bout.

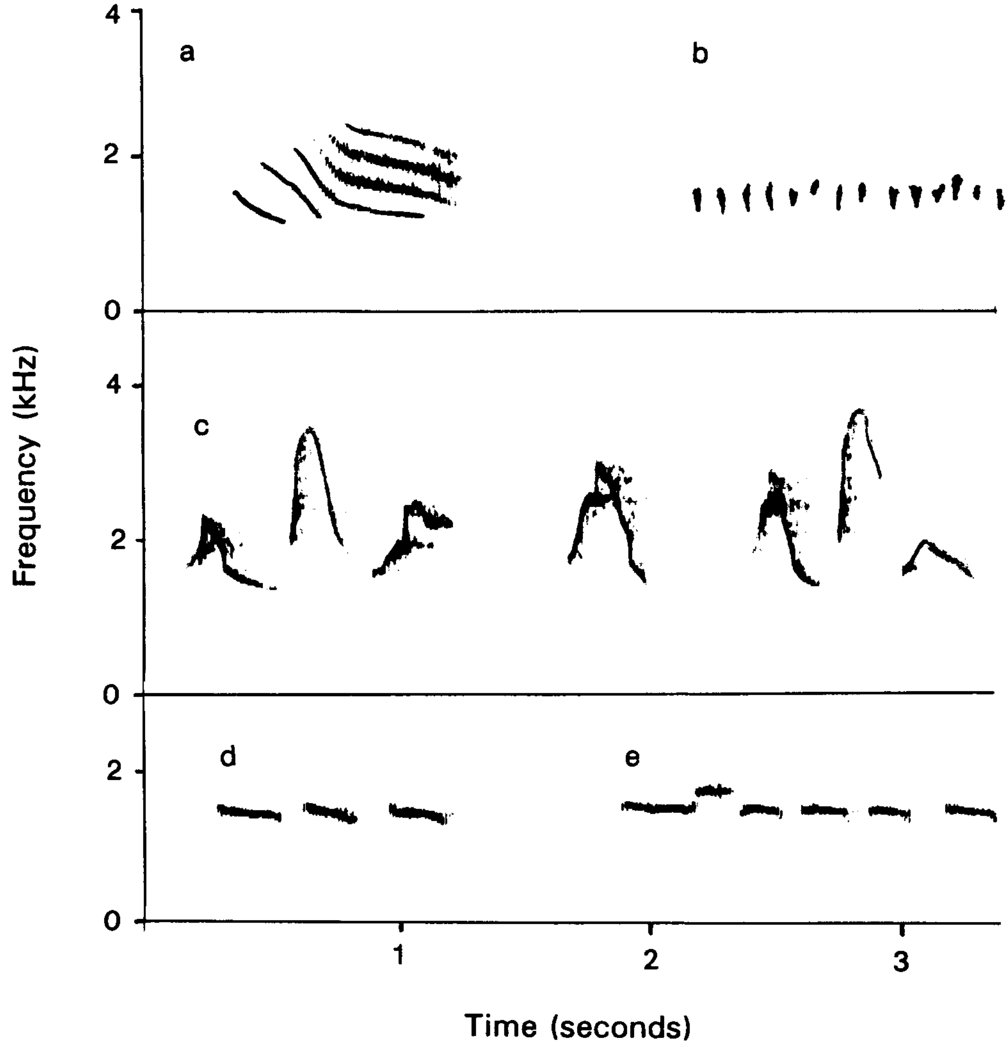

FIGURE 4. Other Vocalizations. (a) *waanh,* (b) *chitter,* (c) seven *wheeoo* calls, (d) one *doodoodoo* call, (e) one *toodleloo* call.

Wheeoo—a brief, moderately loud call (Fig. 4c) given during mobbing choruses directed at potential predators such as the Mottled Owl (*Ciccaba virgata*) and experimentally presented snakes made of modeling clay (McDonald 1993a). *Wheeoo* choruses also occurred during experimental presentation of taxidermically mounted specimens of male manakins. Such choruses often persisted for several minutes and attracted a variety of other species including Stripe-tailed Hummingbirds (*Eupherusa eximia*), Golden-crowned Warblers (*Basileuterus culicivorus*), and Orange-billed Nightingale-Thrushes (*Catharus aurantiirostris*). During presentations of the model snake, but not of the manakin mounts, the other species remained in the vicinity of the threatening stimulus and joined the chorus. *Wheeoo* choruses almost invariably involved three or more male Long-tailed Manakins, and resulted in calling rates of as many as 100 *wheeoo* calls per minute.

Chitter—a soft trill given infrequently in the subcanopy by a lower-ranking male to a dominant male (Fig. 4b). Almost invariably, the call was given by a predefinitive male as a response to chases or other agonistic behaviors directed at them by a definitive male.

Squawk—a squawking or screeching call given

TABLE 3. Call transition matrix: frequency of occurrence and expected values (in parentheses).

Preceding call type	Following call type						
	Toledo	*Wit*	*Owng*	*Teeamoo*	*Weet*	*Waanh*	*Wheeoo*
Toledo	—	26 (28.7)	15 (5.4)*	4 (28.3)*	12 (14.5)	72 (53.7)*	8 (7.1)
Wit	64 (43.5)*	—	25 (7.3)*	29 (40.6)*	30 (20.8)*	40 (77.1)*	11 (9.5)
Owng	6 (7.5)	26 (7.1)*	—	2 (7.0)*	1 (3.6)	5 (13.3)*	0 (1.7)
Teeamoo	5 (41.6)*	33 (39.5)	0 (7.2)*	—	26 (20.0)	117 (73.8)*	10 (9.3)
Weet	9 (21.8)*	28 (20.7)	0 (3.7)*	45 (20.4)*	—	23 (38.7)*	5 (4.8)
Waanh	129 (94.7)*	65 (89.8)*	2 (15.7)*	108 (88.5)*	34 (45.4)*	—	17 (20.4)
Wheeoo	6 (9.8)	17 (9.3)*	0 (1.7)	6 (9.2)	6 (4.7)	17 (17.4)	—

* Transitions for which the departure in the observed from the expected frequencies exceeded a threshold criterion (chi-square, $P \leq 0.05$, df = 1).

by individuals handled in the mist nets. Females tended to give the call more frequently than did males.

SEQUENCE ANALYSIS

Table 3 shows the call transitions for which the observed frequencies showed a major departure from the expected frequencies. Transitions between positively and negatively associated call types are summarized in Table 4. This analysis revealed that calls other than dance calls occurred in two general contexts: during bouts of *toledo* song, and during interactions among males that did not involve courtship of a female. During-song-bout calls were positively associated with *toledo* songs and with one another. These call types include *toledo, wit,* and *owng.* Noncourtship calls, *teeamoo* and *weet,* were positively associated with one another, and usually negatively associated with during-song-bout calls (except *weet* tended to follow *wit*). *Waanh* occurred in both contexts and was positively associated with *toledo* and *teeamoo. Wheeoo* was associated only with *wit.*

PLAYBACK EXPERIMENT

Manakins did not respond to playback of the five call types by singing *toledo* bouts; song occurred in only 19 out of 50 playback periods. For three of the call types, the number of non-zero observations of *toledos* was insufficient to conduct a significance test (Table 5). *Wit* increased significantly during playback of *nyanyownh, teeamoo,* and *weet. Wheeoo* increased during playback of *nyanyownh,* and *wheeoo. Teeamoo* and *weet* increased during playback of several calls, although these increases were not significant. *Wheeoo* was the only playback call to stimulate like calls in response.

DISCUSSION

Analysis of behavioral context and call sequences of the most frequent calls revealed that call types tended to occur in one of three general contexts: during song bouts, during dancing, and during noncourtship interactions. Two vocalizations (*waanh* and *wheeoo*), occurred during both song bouts and noncourtship interactions. One other (*weet*) showed only a weak tendency to occur in noncourtship situations. Detailed observations made during scheduled sample periods allowed us to make inferences about the functions of several of the calls.

DURING-SONG-BOUT VOCALIZATIONS

Toledo—The long, continuous bouts of *toledos,* and their occurrence in the absence of females clearly indicates that the duet song functions as advertisement to attract females to the dance perch. McDonald (1989b) showed that success in attracting females is correlated with singing

TABLE 4. Call transitions that occurred more often (positive call associations) or less often (negative call associations) than expected by chance. The double arrow indicates significance of both transitions in which a call type either precedes or follows the other type. Calls positively associated with toledo songs appear in bold face, calls negatively associated with toledo songs appear in italics, and calls not associated with toledo songs appear in normal type.

Positive call associations	Negative call associations
toledo → **owng**	**toledo** ↔ *teeamoo*
wit → **toledo**	**wit** → *teeamoo*
wit ↔ **owng**	**owng** ↔ *teeamoo*
toledo ↔ waanh	*weet* → **toledo**
teeamoo ↔ waanh	*weet* → **owng**
weet → *teeamoo*	*weet* ↔ waanh
wit → *weet*	**wit** ↔ waanh
wheeoo → **wit**	**owng** ↔ waanh

TABLE 5. Mean number of calls heard during the preplayback and playback periods.

Vocal stimulus	Vocal response: Toledo Pre	Toledo Play	Wit Pre	Wit Play	Teeamoo Pre	Teeamoo Play	Weet Pre	Weet Play	Waanh Pre	Waanh Play	Wheeoo Pre	Wheeoo Play
Toledo	13.9	15.6[a]	14.2	5.8	5.1	8.0	8.1	3.7	6.4	7.8	2.8	1.1
Nyanyownh	16.3	4.3	4.2	26.8*	4.1	6.4	3.0	8.9	1.4	4.2	0.8	11.0*
Teeamoo	0.5	3.6[a]	12.6	41.0*	5.7	8.2	2.4	7.6	3.0	5.8	1.0	1.3[a]
Weet	0.0	4.2[a]	3.3	57.7*	7.0	10.1	3.2	6.1	4.1	4.7	1.3	0.3
Wheeoo	1.2	9.4	6.9	12.6	6.4	5.6	1.4	5.2	3.1	5.7	0.6	11.3*

* Wilcoxon matched-pairs signed-rank test ($P \le 0.002$, $n = 10$).

[a] The number of non-zero samples was insufficient to conduct the significance test.

persistence. Furthermore, females apparently respond to differences in the quality of duets; the rate at which females visit a team of males is correlated with the degree to which the sound frequencies of their songs match one another (Trainer and McDonald, unpubl. observ.).

Wit—Virtually all *toledo* bouts were preceded by a series of *wit* calls given alternately by the two male partners Apparently these calls function to synchronize the behavior of partners just before a bout of *toledo* duets. It also functions in conjunction with *owng* as described below.

Owng—This call probably signals a male's excitement in the presence of a female. Males give *owngs* when they are prepared to dance for a female but the partner is absent, or when a female is present but has not moved to the dance perch. In combination with soft, slower series of *wits* it seems to act to incite females to move to the dance perch for solo male dance displays.

DANCE VOCALIZATIONS

Nyanyownh—This call is the vocal component of the leapfrog portion of the dance display. It probably functions to enhance the display and stimulate the female. Although it is a loud vocalization, it does not appear to function in attracting males or females to the dance display.

Buzz-weent—This call signals the superior dominance status of the male to his dance partner. *Buzz-weent* occurs only in the ritualized context of leapfrog or popcorn dance displays, and does not occur in conflict situations that arise infrequently in other contexts.

NONCOURTSHIP VOCALIZATIONS

Teeamoo—A loud vocalization, *teeamoo* is clearly used to attract a singing partner, usually when he is out of visual contact.

Weet—This loud vocalization occurs during song bouts as well as in the context of male-male, noncourtship interactions. It was most often associated with the *teeamoo* call. *Weet* probably serves to indicate mild distress in response to an unwelcome or unexpected stimulus. For example, *weet* increased during playback of four out of five calls, although these increases were not significant.

Waanh—This soft call is used both during song and noncourtship activities, for communication among males in close proximity. It may be used as a contact call to indicate a male's location when he is not otherwise vocalizing.

Doodoodoo and *toodleloo*—Because of the infrequent occurrence of *doodoodoo* and *toodleloo,* the specific behavioral context, sequence associations, and use in response to playback could not be determined. The occurrence of *wit* and *wheeoo* increased after playback of *doodoodoo,* but the interpretation of this result is unclear.

Wheeoo—This call appears to function as a mobbing call used by both male and female manakins in the presence of predators. In addition, *wheeoo* is given by males affiliated with the perch-zone when a strange male appears, and may serve to attract other resident males to investigate. Consistent with a mobbing function, this was the only call that stimulated like calls in response to playback.

Chitter—This call is a submissive signal to an older or more dominant male.

Squawk—This is a distress call, probably used when a manakin is attacked by a predator, as well as in mist nets.

The results of the playback experiment show that manakins do not respond in a typical territorial manner to playback of several vocalizations. Territorial species usually respond to playback of conspecific song by approaching and engaging in countersinging; in some cases they may attack a mount (Petrinovich and Patterson 1981, Ratcliffe and Grant 1985, Weary et al.

1987, Stoddard et al. 1988). Manakins did not approach closely, nor respond by singing *toledos.* Nor did they countervocalize with the tape by responding with the same call type as the stimulus. Only *wheeoo* stimulated like calls in response, but this probably occurred because manakins were stimulated to mob, not because they were countersinging with the tape.

The use of *wheeoo* in response to playback corroborates other evidence that this call serves a mobbing function. When McDonald (1993a) presented taxidermic mounts of male manakins in perch-zones, males responded with mobbing behavior and *wheeoo* calls (though only two physical attacks). McDonald interpreted the mobbing of mounts as a response to strange males that might pose a threat to the established affiliations of males at a perch-zone. In the playback experiment, only the dance vocalization, *nyanyownh,* and *wheeoo* elicited mobbing calls. The sound of dancing might signal the presence of strange or noncooperative males attempting to court females, and stimulate residents to mob. The sound of mobbing may serve to recruit other lek affiliates to mobbing choruses.

Other playback responses illustrate the importance of cooperative relationships among male affiliates. Playback of *toledo, teeamoo* and *weet,* calls that normally occur among perch affiliates, failed to elicit mobbing calls. *Wits* were strongly stimulated by three calls, and *teeamoo* showed increases, though not significant, to four calls. Our contextual observations of these two vocalizations clearly show that they mediate cooperative interactions among males, including the joint song. This suggests that male manakins generally respond to playback by soliciting interaction with an affiliated male.

The Long-tailed Manakin repertoire of 13 call types is unusually diverse compared to those of other species for which complete repertoires have been described. For example, three suboscine species studied by Smith (1967, 1969, 1971) and five oscine species studied by Moynihan (1962a, 1962b, 1963, 1966) have repertoires of 6–8 call types. Some songbird species develop diverse song repertoires composed of several versions of the primary song (Kroodsma 1982, Kroodsma and Canady 1985, Derrickson 1987). However, in species with extremely large song repertoires, acoustically distinct song types seem to play functionally similar roles in communication (Verner 1976, Smith and Reid 1979). Even species in which different song types occur in different behavioral contexts have complete repertoires of functionally distinct vocalizations that are comparable in size to those mentioned above (Smith et al. 1978, Trainer 1987). The large call repertoires of the Long-tailed Manakin may be related to the unique nature of male-male interactions, which, unlike the above territorial species, are characterized by joint display and cooperation in the context of intense sexual selection characteristic of lek mating systems.

The size of the Long-tailed Manakin's vocal repertoire is even more striking when compared with that of other manakins. The revised, monophyletic manakin family, Pipridae, contains 40 species (Prum 1990a, 1992). The behavior of 13 of these species has been described sufficiently to estimate the size of the vocal repertoire. At least 12 species also produce mechanical sounds with special wing feathers (Prum 1990b). The size of the complete acoustic repertoires of manakins varies between 1 and 8 (Snow 1961, 1963a; Skutch 1969; Lill 1974, 1976; Schwartz and Snow 1978; Snow and Snow 1985; Robbins 1983; Prum 1985; Prum and Johnson 1987; Prum 1990b). Some of the repertoire sizes may be underestimates because some species were observed for brief periods or only during the courtship dance. Nevertheless, further study of these species seems unlikely to reveal any repertoire size as large as that of *Chiroxiphia.*

If call diversity were purely a consequence of joint, nonterritorial display, then we would expect large repertoires of acoustic signals in other members of the Pipridae that perform joint displays. A review of the literature, however, does not support this prediction. Besides the four species in the genus *Chiroxiphia,* joint displays by two males have been observed in eight species: *Machaeropterus pyrocephalus, M. regulus* (Sick 1967), *Masius chrysopterus* (Prum and Johnson 1987), *Pipra aureola* (Snow 1963a), *P. coronata* (Skutch 1969), *P. fasciicauda* (Robbins 1983), *P. filicauda* (Schwartz and Snow 1978), *P. serena* (Prum 1985). These species would be expected to have large repertoires of acoustic signals. Repertoire sizes of these species ranged from approximately four to eight, although further study may reveal additional acoustic signals. Apparently, joint display alone is not sufficient to account for large repertoires. The behavior of these manakins differs in several ways from that of *Chiroxiphia,* and this may account for their lack of large repertoires. First, only *Chiroxiphia* manakins have obligate joint displays (Snow 1963b, 1971; Foster 1977, 1981). In the other manakins, solitary displays for females occur on a regular basis and may be more frequent than joint displays. The occurrence of joint displays in these other manakins ranges from very infrequent to frequent but appears never to be obligatory. Second, only *Chiroxiphia* manakins have both joint advertisement and joint dance. In *Pipra fasciicauda,* two males may display to attract a female, but subsequently only the dominant male courts her (Robbins 1985). In the remaining species, males display individually to attract females, usually on dispersed territories, but two males may perform a joint dance display. None of these species has a joint cooperative vocalization, as does *Chiroxiphia.* Finally, the cooperative rather than aggressive function of joint display has been demonstrated only in *Chiroxiphia* (McDonald 1989a, 1989b). To be cooperative, a joint display must involve investment by more than one male in attracting or exciting females during courtship (Prum and Johnson 1987). Whether joint displays are cooperative in this sense is unknown for most manakin species (Snow 1963b, Sick 1967, Prum and Johnson 1987). A cooperative function of display is questionable in *P. coronata* and *P. serena* because joint displays may be more prevalent during the nonbreeding season or in the absence of females than during courtship (Skutch 1969, Prum 1985). Prum (1985) suggested that *P. serena* joint displays are probably aggressive rather than cooperative because they are performed by two males that occupy different territories, and they usually occur during countersinging when no females are present.

We suggest that the diversity of the Long-tailed Manakin vocal repertoire is related to the complex, nonterritorial, cooperative social system. Each male maintains a network of relationships with several other males that persists for a number of years (McDonald 1989a). These long-term, cooperative relationships may favor the evolution of diverse communication signals. At least 10 of the Long-tailed Manakin call types function in communication among males; they are directed at males or occur in the absence of females. It may be that excluding males from a territory does not require as many functionally distinct call types as does cooperation. Among manakins, joint display in the absence of cooperation appears not to be associated with large repertoires. Further study of the relationship between vocal behavior and social organization in manakins is warranted.

ACKNOWLEDGMENTS

This project was funded by NSF grant BNS-8814038 to JMT, a Jessie Smith Noyes Foundation grant from the Organization for Tropical Studies, The Frank M. Chapman fund of the American Museum of Natural History and the American Philosophical Society. DBM is grateful to the Harry Frank Guggenheim Foundation, the Organization for Tropical Studies and the National Geographic Society for support. Joe and Jean Stuckey graciously permitted the use of their farm as a study site. Members of the Monteverde community have helped in many ways. Personnel in the offices of Vida Silvestre were remarkably courteous, prompt and helpful in securing necessary permits. We would like to thank Alberto Hernandez for help translating the abstract, and Mercedes S. Foster and Richard O. Prum for comments on the manuscript.

LITERATURE CITED

ATWOOD, J. L., V. L. FITZ, AND J. E. BAMESBERGER. 1991. Temporal patterns of singing activity at leks of the White-bellied Emerald. Wilson Bull. 103:373–386.

BRADBURY, J. W. 1981. The evolution of leks, p. 138–169. *In* R. D. Alexander and D. W. Tinkle [eds.], Natural selection and social behavior: recent research and new theory. Chiron, New York.

BRADBURY, J. W., S. L. VEHRENCAMP, AND R. M. GIBSON. 1989. Dispersion of displaying male Sage Grouse. 1. Patterns of temporal variation. Behav. Ecol. Sociolbiol. 24:1–14.

DERRICKSON, K. C. 1987. Yearly and situational changes in the estimate of repertoire size in Northern Mockingbirds (*Mimus polyglottos*). Auk 104: 198–207.

FOSTER, M. S. 1977. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis.* Amer. Natur. 11: 845–853.

FOSTER, M. S. 1981. Cooperative behavior and social organization of the Swallow-tailed Manakin. (*Chiroxiphia caudata*). Behav. Ecol. Sociobiol. 9:167–177.

GOODMAN, L. A. 1968. The analysis of cross-classified data: independence, quasi-independence, and interactions in contingency tables with or without missing entries. J. Am. Statist. Assoc. 63:1091–1131.

HOLDRIDGE, L. 1966. The life zone system. Adansonia 6:199–203.

KROODSMA, D. E. 1982. Song repertoires: problems in their definition and use, p. 125–146. *In* D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds, vol. 2. Academic Press, New York.

KROODSMA, D. E., AND R. A. CANADY. 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among Marsh Wren populations have a genetic basis. Auk 102:439–446.

LEMON, R. E., AND C. CHATFIELD. 1971. Organisation of song in Cardinals. Anim. Behav. 19:1–17.

LILL, A. 1974. Sexual behavior of the lek-forming White-bearded Manakin (*M. manacus trinitatus* Hartert). Z. Tierpsychol. 36:1–36.

LILL, A. 1976. Lek behavior in the Golden-headed Manakin, *Pipra erythrocephala,* in Trinidad (West Indies). Z. Tierpsychol. Adv. Ethol. 18.

MCDONALD, D. B. 1989a. Cooperation under sexual selection: age-graded changes in a lekking bird. Amer. Natur. 134:709–730.

MCDONALD, D. B. 1989b. Correlates of male mating success in a lekking bird with male-male cooperation. Anim. Behav. 37:1007–1022.

MCDONALD, D. B. 1993a. Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. Ethology 94:31–45.

MCDONALD, D. B. 1993b. Demographic consequences of sexual selection in the Long-tailed Manakin. Behav. Ecol. 4:297–309.

MOYNIHAN, M. 1962a. Display patterns of tropical American "nine-primaried" songbirds. I. *Chlorospingus.* Auk 79:310–344.

MOYNIHAN, M. 1962b. Display patterns of tropical American "nine-primaried" songbirds. II. Some species of *Ramphocelus.* Auk 79:655–689.

MOYNIHAN, M. 1963. Display patterns of tropical American "nine-primaried" songbirds. III. The Green-backed Sparrow. Auk 80:116–144.

MOYNIHAN, M. 1966. Display patterns of tropical American "nine-primaried" songbirds. IV. The Yellow-rumped Tanager. Smithsonian Miscellaneous Collection 140(5):1–34.

PETRINOVICH, L., AND T. L. PATTERSON. 1981. The responses of White-crowned Sparrows to songs of different dialects and subspecies. Z. Tierpsychol. 57:1–14.

PRUM, R. O.. 1985. Observations of the White-fronted Manakin (*Pipra serena*) in Suriname. Auk 102: 384–387.

PRUM, R. O. 1990a. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. Occ. Pap. Mus. Zool. Univ. Michigan 723:1–44.

PRUM, R. O. 1990b. Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves: Pipridae). Ethology 84:202–231.

PRUM, R. O. 1992. Syringeal morphology, phylogeny, and evolution of the neotropical manakins (Aves: Pipridae). Amer. Museum Notitates 3043:1–65.

PRUM, R. O., AND A. E. JOHNSON. 1987. Display behavior, foraging ecology, and systematics of the Golden-winged Manakin (*Masius chrysopterus*). Wilson Bull. 99:521–539.

RATCLIFFE, L., AND P. GRANT. 1985. Species recognition in Darwin's finches (*Geospiza* Gould). III. Male responses to playback of different song types, dialects, and heterospecific songs. Anim. Behav. 33:290–307.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROBBINS, M. B. 1983. The display repertoire of the Band-tailed Manakin (*Pipra fasciicauda*). Wilson Bull. 95:321–342.

ROBBINS, M. B. 1985. Social organization of the Band-tailed Manakin (*Pipra fasciicauda*). Condor 87: 449–456.

SCHWARTZ, P., AND D. W. SNOW. 1978. Display and related behavior of the Wire-tailed Manakin. Living Bird 17:51–78.

SICK, H. 1967. Courtship behavior in manakins (Pipridae). J. Ornith. 100:269–302.

SKUTCH, A. F. 1969. Life histories of Central American birds. III. Pacific Coast Avifauna 35:1–580.

SLATER, P.J.B. 1973. Describing sequences of behavior, p. 131–153. *In* P. B. G. Bates and P. H. Klopfer [eds.], Perspectives in ethology. Plenum Press, New York.

SMITH, D. G., AND F. A. REID. 1979. Roles of the song repertoire in Red-winged Blackbirds. Behav. Ecol. Sociobiol. 5:279–291.

SMITH, W. J. 1967. Displays of the Vermilion Flycatcher (*Pyrocephalus rebinus*). Condor 69:601–605.

SMITH, W. J. 1969. Displays of *Sayornis phoebe* (Aves Tyrannidae). Behaviour 33:283–322.

SMITH, W. J. 1971. Behavioral characteristics of serpophaginine tyrannids. Condor 73:259–286.

SMITH, W. J., J. PAWLUKIEWICZ, AND S. T. SMITH. 1978. Kinds of activities correlated with singing patterns of the Yellow-throated Vireo. Anim. Behav. 26: 862–884.

SNOW, D. W. 1961. The displays of the manakins *Pipra pipra* and *Tyranneutes virescens.* Ibis 103: 110–113.

SNOW, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus,* in Trinidad. Zoologica 47:65–104.

SNOW, D. W. 1963a. The display of the Orange-headed Manakin. Condor 65:44–48.

SNOW, D. W. 1963b. The display of the Blue-backed Manakin, *Chiroxiphia pareola,* in Tobago, W. I. Zoologica 48:167–176.

SNOW, D. W. 1971. Social organization of the Blue-backed Manakin. Wilson Bull. 83:35–38.

SNOW, D. W. 1977. Duetting and other synchronised displays of the Blue-backed Manakins, p. 239–251. *In* B. Stonehouse and C. M. Perrins [eds.], Evolutionary ecology. University Park Press, Baltimore.

SNOW, B. K., AND D. W. SNOW. 1985. Display and related behavior of male Pin-tailed Manakins. Wilson Bull. 97:273–282.

STODDARD, P. D., M. D. BEECHER, AND M. S. WILLIS. 1988. Response of territorial male Song Sparrows to song types and variations. Behav. Ecol. Sociobiol. 22:125–130.

TRAINER, J. M. 1987. Behavioral associations of song types during aggressive interactions among male Yellow-rumped Caciques. Condor 89:731–738.

TRAINER, J. M. 1988. Singing organization during aggressive interactions among male Yellow-rumped Caciques. Condor 90:681–688.

VERNER, J. 1976. Complex song repertoires of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14:263–300.

WEARY, D. M., R. E. LEMON, AND E. M. DATE. 1987. Neighbour-stranger discrimination by song in the Veery, a species with song repertoires. Can. J. Zool. 65:1206–1209.