COOPERATION UNDER SEXUAL SELECTION: AGE-GRADED CHANGES IN A LEKKING BIRD

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In many mating systems, particularly lekking systems, the variance of male mating success is often high, providing an opportunity for strong sexual selection (Wade and Arnold 1980). Indeed, in lekking systems, mating success may be the single most important component of male fitness. The elaborate, cooperative, dual-male courtship displays in the leks of long-tailed manakins (*Chiroxiphia linearis*, Aves: Pipridae) have long intrigued biologists (Nutting 1884; Slud 1957; Foster 1977). Because sexual selection is characterized by intense competition among males for mates, the juxtaposition of such competition with male-male cooperation presents an apparent paradox. How and why do partnerships develop? Benefits to cooperation might include indirect (kin) selection (Hamilton 1964; J. L. Brown 1978) or reciprocity (Trivers 1971; Ligon and Ligon 1978; Axelrod and Hamilton 1981). Kin-selection theory predicts that cooperators should be more closely related than should pairs of randomly selected males from within the same local populations. Reciprocity does not require relatedness. It does, however, require nonrandom associations, with a high frequency of encounter among potential cooperators (J. S. Brown et al. 1982). Age-graded queuing for status (Wiley and Rabenold 1984) may be viewed as a particular form of reciprocity in which the benefits are highly asymmetrical in time. A mechanism for such queuing could be the establishment and maintenance of dominance hierarchies based primarily on age (Foster 1981).

Male long-tailed manakins undergo a 4-yr process of plumage maturation, which is unusually long for a passerine bird (Lawton and Lawton 1986). Plumage maturation in the largest genera of manakins, *Pipra* and *Manacus*, requires no more than 2 yr in the best-studied species (Snow and Lill 1974) and may occur in the year after hatching in other genera (Skutch 1967). A number of different hypotheses exist to explain delayed plumage maturation in temperate passerine birds (Selander 1972; Rohwer et al. 1980; Lyon and Montgomerie 1986). Both delayed plumage maturation (Procter-Gray and Holmes 1981) and cooperation (Woolfenden and Fitzpatrick 1984) have been described as strategic responses to

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limited opportunities for present reproductive success. Limited present opportunities should engender long-term strategies aimed at enhancing future success. In this paper I describe age-graded changes in male behavior and morphology and the pattern of variance of male copulatory success that accompanies the formation of male partnerships in long-tailed manakins. I discuss these results in terms of a response by younger males to limited opportunities for present reproductive success.

Leks consist of a core partnership between an alpha and a beta male, plus a variable number of affiliates. For courtship display, two males, usually the alpha and beta but occasionally other combinations of affiliates, give a call in unison that phonetically resembles the word "toledo." On the arrival of a female, both males and the female move to a low dance perch and the males begin a dance display comprising backward leapfrog hops alternating with labored "butterfly" flight. Dances with a female present have a distinctive rhythm of hops and butterfly flight. Displays in the absence of females often include bouts of "popcorn" hops, in which two or more males hop side by side rather than leapfrogging. Dances leading to copulations included a solo butterfly flight by the alpha male. Elsewhere, I describe the courtship displays in more detail (McDonald 1989). A perch zone was defined as the area, sometimes containing several dance perches, within which a particular alpha male was dominant. Although perch zones were rather uniformly distributed throughout the study area, large areas of suitable habitat were rarely or never used by displaying males, and each perch zone included a cluster of displaying males. Thus, the system conforms *spatially* to Bradbury's (1981) definition of a lek.

<center>MATERIALS AND METHODS</center>

The study area, in Monteverde, Costa Rica (10°18′N, 84°48′W), is 80 ha of premontane tropical moist forest (Holdridge 1966) at 1300 m elevation. Previous studies have been done by Foster (1976, 1977, 1981, 1987) in the drought-deciduous lowlands of Guanacaste Province, Costa Rica, on long-tailed manakins and in Paraguay on the swallow-tailed manakin, *Chiroxiphia caudata*. Snow (1971) briefly studied another congener, *C. pareola*, on Tobago.

During periodic mist-netting sessions birds were weighed with a 50-g Pesola ™ scale to the nearest 0.5 g. All weights were from birds netted from March to July, except for the weights of nonbreeding birds recorded in October 1987. For the analysis of weight data, male status refers to the status at the time of weighing, not to eventual status. Testis volume was measured on fresh specimens using the formula for the volume of an ellipsoid, $\frac{4}{3} \pi ab^2$ (Foster 1987). I color-banded 270 long-tailed manakins in the study area from 1981 to 1987. Of these, 69 were known to be females because they had vascularized brood patches (males also have an abdominal apterium), because they remained in green plumage for more than two seasons, or because they exhibited female-like behavior during dance displays by males. Of the remainder, 116 were males, and 85 were of unknown sex (i.e., were captured in green plumage and did not have vascularized brood patches or visitation histories). Of the 85 birds of unknown sex, 30 were suspected of being female because of elevated weights or the extent of brood-patch defeathering. As

in other manakins (Snow and Lill 1974), life span is probably 12 yr or more, and females probably begin breeding the year after hatching (Foster 1976; Lill 1976). Males may display at low levels as early as January and as late as October, with the peak from mid-April to early June.

Alpha males could be recognized by the following criteria. (1) During displays for females, the alpha male sometimes ended sets of hops by facing his male partner, turning his tail toward the female(s), and giving a sharp "weent" call. Other males did not direct these calls at alpha males, but such calls were given by beta males toward other males and by definitive males toward subdefinitives, usually when no female was present. (2) Alpha males remained for solo display and copulation, if a female remained long enough following a dual-male display. (3) Alpha males gave at least 80% of the "teeamoo" calls, which function as partner attractants in male-male communication. (4) Alpha males had the highest attendance rates of any male in the leks. Of the alpha males in this study, two were never seen performing solo display for females; all the others fit all four criteria. Perch zones included one to four alternative dance perches, of which only one or two were generally used for displaying to females. Adjacent perch zones (75–300 m apart) were often in auditory but never in visual contact.

Observations from six major perch zones (fig. 1) provided the bulk of the results from 1983 to 1986. Eight minor perch zones were sampled less intensively during the 4-yr period and had sporadic activity levels; most of these eight zones received few, if any, female visits. Observation periods lasted 2 h and were conducted from blinds 8–12 m from the dance perch. Since all-day observations (5:30 A.M.–5:30 P.M., $N = 22$) and late-afternoon observations revealed little male display and rare female visitation after 3:00 P.M., beginning times in each perch zone were from 6:00 A.M. to 1:00 P.M. Usually only one dance perch per zone was monitored at any given time, but two to six observers watched different perch zones simultaneously for 83% of the 2-h observations. All major calls could be noted from any blind in a zone. The predominance of a single perch as the dance perch for female visits, and the distinctive rhythm of sounds from displays for females, made it unlikely that female visits to other perches in a zone went unrecorded. Although the order of observations was randomized, I constrained scheduling so that more-active perch zones were more heavily sampled than were less active ones. I corrected for uneven sampling effort by using the appropriate statistical tests. Observers monitored 22 variables describing male and female attendance and behavior. From 1983 to 1986, 2456 h (1216 in 1985) of 2-h observations were conducted in 22 blinds (8 major and 14 minor). During that period, 55 banded males and 27 banded females displayed in perch zones or attended them. Field seasons extended throughout April, May, and June (the peak months), but in two of the years they lasted from early March until the end of July.

RESULTS

Maturation of Plumage and Testes

Male long-tailed manakins move through a 3-yr sequence of subdefinitive plumages before attaining definitive male plumage at age four. I captured or sighted five
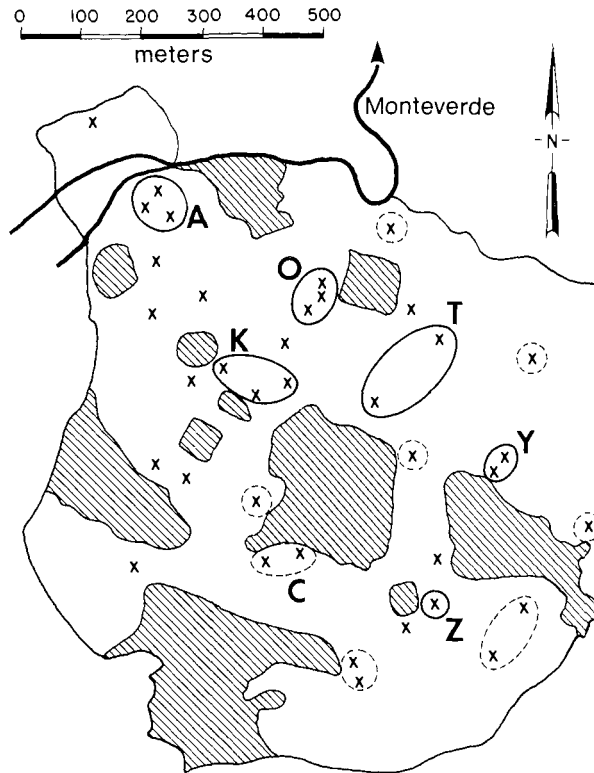
FIG. 1.—Diagram of study area in Monteverde, Costa Rica, for study of long-tailed manakins, 1981 to 1987. x, Dance perches; *unbroken ellipses* with alphabetical labels, the six major perch zones; *dashed ellipses*, minor perch zones; *hatching*, pasture.

banded males in each of the four years of the maturation sequence and have data for two or more successive years for an additional 22 banded subdefinitive males. Since I never followed fledglings, I am assuming that the first unambiguously male plumage (red cap) occurs in the next breeding season after hatching (Foster 1987). The year after hatching, males (red cap) have variably red caps and may have somewhat elongated central tail feathers (rectrices) that extend 4–9 cm beyond the other rectrices. Two years after hatching, the males (dark face) have a dark mask and a full red cap. The final subdefinitive plumage (blue back) includes darkened body plumage, blue feathers on the back, and often full-length central rectrices (10–17 cm). The amount of green in the plumage of the wings, back, and body is variable, but most blue backs are distinguishable in the field from males in definitive plumage. The definitive, "adult" plumage is black with a powder-blue back, full red cap, and long central rectrices. My conclusions differ from those of Foster (1987) in referring the blue-back plumage to a single year class (3 yr after hatching) and in placing red-cap and dark-face males in separate age classes (1 and 2 yr after hatching, respectively). Because birds could hatch from February to October, some caution is warranted in describing plumage sequences by age.
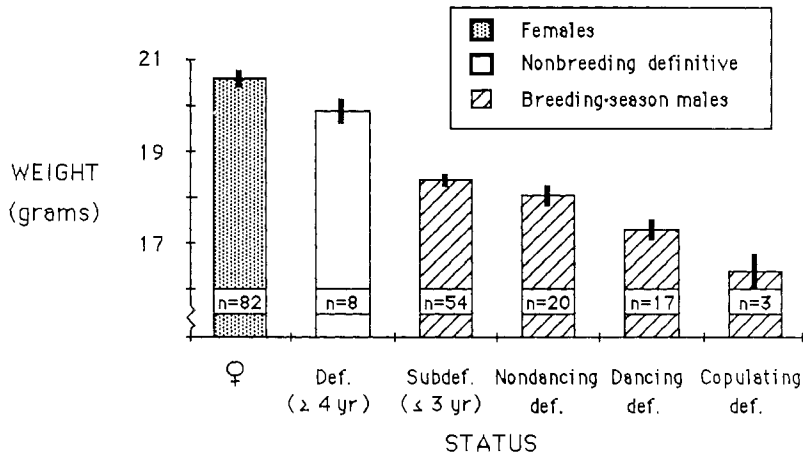
FIG. 2.—Weights of long-tailed manakins by sex, age, and status. Categories of breeding-season males: *Subdef.*, males in subdefinitive plumage; *Nondancing def.*, males in definitive plumage that did not dance for females; *Dancing def.*, males that danced for one or more females; *Copulating def.*, males that copulated with one or more females. Bars show one standard error above and below the mean.

Birds hatched late in the season might more closely resemble those in the next cohort than those in their own cohort hatched at the beginning of the season. These factors may help reconcile Foster's and my sequences. Neither between-season comparisons for individual males nor cross-sectional analysis of males by age or status category indicates an increase in tail length with age in definitive males; nor does plumage brightness appear to differ among definitive males.

I have data on testis size for only one definitive male of known status. This male was either an alpha or a beta in perch zone K in 1982 and was killed in a mist net by an avian predator in 1983. His testis volume was 78.5 mm^3, which is three standard deviations above the mean (29.3 mm^3 $\pm$ 16.2, N = 60), but within the range (7.3–104.7), for males in definitive plumage in a study by Foster (1987). Perch zone K received female visits in 1982, but no copulations were observed there.

Changes in Weight

Weights of long-tailed manakins differed among sex, age, and status categories (fig. 2). Breeding-season weights of males are arranged in four mutually exclusive categories based on status at the time of weighing: (1) males in subdefinitive plumage ($\leq$ 3 yr of age); (2) definitive males ($\geq$ 4 yr of age) never seen dancing for a female; (3) males that had been seen dancing for females but not copulating; and (4) males seen copulating. Also plotted are weights of definitive males during the nonbreeding period. Female weights were significantly greater than any breeding-season weights of males (P < 0.01; all weight tests by GT2-method, Sokal and Rohlf 1981). The female weights might reflect a change caused by carrying eggs, which can greatly increase female weights (see, e.g., Vehrencamp et al. 1986).

Weights of females with vascularized brood patches ($\bar{x}$ = 20.5 g ± 1.4, N = 54), however, did not differ from those of non-vascularized females ($\bar{x}$ = 20.8 g ± 1.3, N = 22), suggesting that the sexual difference was not due solely or primarily to carrying eggs. Males in subdefinitive plumage (≤3 yr old) were significantly heavier than were dancers (P < 0.01) or males that copulated (P < 0.01). The lightest weights measured, 16.0 g, included that of a highly successful male in perch zone Z at the end of the 1984 season. His weight was 78% of the mean weight for females. Since this male was present, and a top performer, in 1985, 1986, and 1987, the low weight had no apparent effect on his survival over a 3-yr period. The sexual weight difference is seasonal, since males gain weight during the nonbreeding season. The weights of females and of nonbreeding definitive males (shown in fig. 2) were significantly greater than the breeding-season weights of definitive males (17.6 g ± 0.9, N = 42; both P < 0.01) but did not differ from each other. Individuals captured repeatedly showed the same patterns shown by the overall categories, which were based primarily on single captures of males in different categories. An alpha male successful in copulating, for example, weighed 20 g in the nonbreeding season, as compared with a mean of 17.2 g for his two breeding-season captures. In contrast to the breeding-season pattern, the non-breeding-season pattern was that definitive males were heavier than nonbreeding subdefinitive males ($\bar{x}$ = 19.2 g ± 0.5, N = 10, P < 0.05).

Age Structure and Survival Rates in Male Groups

The annual disappearance rate of males in definitive plumage (≥4 yr of age) with histories as affiliates from 1983 to 1987 ranged from 9% to 23%. The latter figure will be reduced if birds not sighted in 1987 are resighted in succeeding years. Younger, especially subdefinitive, males that were not resighted may have settled outside the study area, given the large distances between perch zones in which males can be affiliates (see "*Spatial Affiliations of Males,*" below). For older males (≥6 yr old), disappearance rates probably closely reflect mortality. Until more is known of male dispersal and settlement, estimates of survival rates based on disappearance rates among younger males will be unreliable. Only males banded in subdefinitive plumage (≤3 yr old) could be aged. Of the banded males sighted in perch zones each year, a growing number and proportion were of known age between 1983 (3 of 20 banded affiliates of known age) and 1986 (24 of 36). Through 1984, none of the 23 banded, known-age males (range, 1–6 yr old) was seen dancing for a female. In 1985, 4 of 20 banded males (20%) that danced for females were of known age; their dances accounted for 2% of the total duration of female visits. On the two occasions, 3-yr-old males danced for females, but these subdefinitive males were supplanted by definitive males within 30 s. In 1986, 4 of the 10 males (40%) that danced for females were of known age (5–8 yr old); their dances accounted for 9% of female visitation time. Four of the males (5–7 yr old) danced for a female that left in less than 2 min, or they were replaced during a dance by dominant males of unknown age (two were at least 7 yr old). Only the fifth male, the 8-yr-old, appeared to be a beta male in a moderately successful perch zone. None of 15 other known-age definitive males, ranging from 4 to 7 yr of

TABLE 1

COPULATORY SUCCESS OF MALE LONG-TAILED MANAKINS

	MALE/PERCH ZONE							
	1/Z	2/A	3/Y	4/A	5/C	6/O	7/T	8(beta)/Z
1983								
Rate	—	0.11	—	0	—	0	—	—
No.	—	3 (6)	—	0	—	0	—	—
%	—	100	—	0	—	0	—	—
1984								
Rate	0.31	0.02	0	0.02	—	0.02	0	0
No.	17 (15)	1	0	1	—	1 (1)	0	0
%	84	5	0	5	—	5	0	0
1985								
Rate	0.36	*	0.06	0.03	0	0	0.02	0.02
No.	43 (6)	*	5 (1)	3 (1)	0	0	1 (1)	2
%	74	*	12	6	0	0	4	4
1986								
Rate	0.09	*	0.03	*	0.04	0	0	*
No.	3 (2)	*	1	*	1	0 (1)	0 (1)	*
%	56	*	19	*	25	0	0	*
% of 4-yr summed rates	67	12	8	4	4	2	2	2

NOTE.—The rate is the number of copulations per 2-h observation period. No males other than the eight listed here were seen to copulate. The numbers of copulations shown in parentheses were excluded for reasons given in the text. Copulatory success is computed as the percentage of the summed rates, because sample sizes were unequal. Missing data (dashes) indicate that males were not monitored in that year.

* Males that are presumed to have died.

age, held a rank higher than gamma in any of the 14 monitored perch zones in the study area. Thus, males appear to be at least 8 yr of age before attaining beta status.

Both the age of establishment and the duration of tenure as an alpha male affect the age structure of the group of males affiliated with a lek. I have seen three ascents to alpha status, all by the male that had previously held the beta role. A banded alpha male displaying outside my study area was successful in copulating in 1982, 1983, 1984, and 1985 but disappeared after the 1985 season, at which time he was at least 10 yr of age (pers. obs.; R. LaVal and R. Law, pers. comm.). Minimum ages of other alpha males (all banded as definitives) ranged from 7 to 9 yr in 1987. Since these males were all well established (often as alpha males) at the time of banding, most are almost certainly at least 4–6 yr older than the minimum. The highly successful alpha male in perch zone Z had a minimum tenure of 4 yr (1984–1987), as did four other alpha males. The beta male that assumed the alpha role in perch zone A in 1984 disappeared between July 1985 and April 1986. His tenure, therefore, was one and a half seasons. At least one female that visited during the tenure of the preceding alpha male (male 2, table 1) returned to visit the new alpha (male 4, table 1). If an alpha male's tenure is generally 2–4 yr and an 8-

yr-old beta male must wait for turnover, then males may be 10–12 yr of age before attaining alpha status. Most males begin at least occasional attendance in perch zones while still in subdefinitive plumage.

Male-Male Interactions

Although agonistic encounters, including chases and displacements, occurred among males during displays, particularly when three or more males and no females were present, I found no evidence of territoriality. Males in any plumage state were tolerated in perch zones except during female visits, when either the alpha male or his partner, or both, chased any lower-ranking male that appeared in the vicinity of the perch ($N = 6$, during 272 dual-male dances for females). Thus, male interactions determine dominance ranks and influence the development of alliances among affiliates rather than excluding some males from a lek. Only high-ranking males had the prospect of performing for females. If a male began a display in the absence of a higher-ranking affiliate (e.g., a gamma male dancing with the alpha male for a female), and the higher-ranking male returned during the course of the dance, he replaced the lower-ranking male ($N = 14$). For all cases in which a dual-male dance progressed to the solo stage that precedes copulation, it was always the alpha male who remained ($N = 153$, 7 different alpha males). Alpha males performed all but 2 of 117 copulations. The exceptions are discussed in the section on the variance of copulatory success. When more than two males began a dance and one was chased away, it appeared that females tolerated multiple males but were scared off by the agonism among males, which occurred on the dance perch ($N = 3$). Thus, females do not have the option of choosing within a lek but do appear to be able to choose among leks. Although alpha males chased away any male that appeared in the vicinity of the perch during solo display ($N = 13$ during 153 solos), they usually did so away from the dance perch itself, on first sighting a potential intruder. I found no evidence of a disruption of copulations, since 7 of the 13 intrusions were followed by copulations by the alpha male. This proportion does not differ from that of undisturbed solo flights leading to copulations. Foster (1983) found a similar lack of disruption among long-tailed manakins but noted disruptions among the congeneric swallow-tailed manakin.

Variance of Male Mating Success

From 1983 to 1986, 117 copulations were observed. I excluded 39 of these from certain of the analyses, including those in table 1, for one or more of the following reasons: (1) they occurred outside the study area ($N = 4$); (2) they did not occur during a formal observation period ($N = 33$); and (3) they could have been copulations between the same individuals on the same day ($N = 5$). Perches receiving female visits had high mean rates of unison "toledo" calling (≥ 250 "toledos"/2 h; McDonald 1989). Because my sampling included several perch zones with low "toledo" output that did not receive female visits, I am confident that I sampled all males with even slight probabilities of copulating. Estimating from the observed rate, the alpha male in perch zone Z performed 67% of all the copulations in the study area from 1983 to 1986 (table 1). Only 8 of 85 males monitored during the 4 yr of intensive coverage were known to have copulated

TABLE 2

SAMPLING EFFORT AND MEASURES OF MATING SUCCESS FOR MALE LONG-TAILED MANAKINS

	1983	1984	1985	1986	Cumulative
Sampling effort	210 h	510 h	1216 h	520 h	2456 h
Perch zones monitored	3	6	6 (+ 5 minor)	6 (+ 8 minor)	6 (+ 8 minor)
Banded males	20	33	36	36	55
Unbanded males	8	15	19	22	30
Successful/total					
number of males	1/28	4/48	5/55	3/58	8/85
I_S (method 1)	28.0	31.5	28.6	15.8	37.2
I_S (method 2)	28.0	33.2	31.7	22.9	39.8

NOTE.—The estimate of the number of unbanded males was computed by summing records of unbanded males zone by zone and then dividing by the mean number of zones attended by banded males. Because perch zones could be monitored and males could be sighted in two or more years, cumulative values do not necessarily equal the sum of annual values. Computation methods for I_S, the opportunity for sexual selection, and cautions for its use, are given in the text.

(table 2). Four of these males accounted for over 90% of all the copulations. By extrapolating from the number of distinguishable females with whom he copulated during observations, I estimate that the most successful alpha male (in perch zone Z) mated with as many as 50 different females during each of the 1984 and 1985 seasons. All females ($N = 7$) that copulated on more than one day within a season did so with the same male.

To estimate the variance of mating success, I transformed the number of copulations into an estimate of the number of female mates in order to compute I_S (Wade and Arnold 1980), which equals the variance of the number of mates divided by the square of the mean. I estimated the number of mates by adjusting the number of copulations by unbanded females. For the adjustment factor, I used the mean number of times ($\bar{x} = 2.1$) that banded females were seen to return for copulations during the most heavily monitored season (1985, 260 h) in the most successful perch zone. I then used two methods for computing I_S. Method one used the estimates of the numbers of mates without adjusting for unequal sampling. Method two assumed a mean of one mate per male for three reasons. (1) The sex ratio does not appear to differ from 1:1, and I assume that all females mate and that mating males produce viable sperm. Any reproductive failure after fertilization comes under the heading of I_f, the opportunity for selection to act on female reproductive success (Wade and Arnold 1980). (2) The range of male success in the study appears to be representative of male success on a larger scale (see below; i.e., the study area can be viewed as a local population, and each zygote has one male and one female parent). (3) If low sampling intensity produces a mean less than one, I_S can artificially assume a high value (Downhower et al. 1987). Using a mean of one mate per male, the allocation of mates then followed the percentage of copulations given in table 1, which adjusted for unequal sampling. Although the values of I_S that I have computed (table 2) are considerably higher than any listed by Payne (1984), any such measure of the variance of mating success should be treated with considerable caution in making interspecific comparisons because of its dependence on sampling scope and inten-

sity (Kluge 1981; Trail 1985; Downhower et al. 1987). Further, for I_S calculated over more than one season, survival rate becomes a component of mating success, and natural and sexual selection are confounded (S. J. Arnold, pers. comm.).

On two occasions in 1985, the beta male in perch zone Z copulated with a female, in the absence of the alpha male. These copulations followed solo "butterfly" flight and were not immediately preceded by dual-male display. In three of the seven instances of such solo copulations by alpha males, the females had copulated in that perch zone earlier that day or on the preceding day (I recognized the particular females by their bands or tawny feathering in the crown, which is present in less than 25% of females and often differs among females in placement and extent). Thus, I suspect that the beta male copulated with females that had recently copulated with the alpha male, and the beta male's copulation may have effected only partial fertilization of a clutch. Nevertheless, occasional copulations would be a powerful short-term incentive to cooperation in a species with such a high variance of mating success. Beta males may also benefit from the tendency of females to return to the same perch zone in succeeding years. At least one banded female known to have visited under the tenure of the preceding alpha male visited the beta male that assumed the alpha role in perch zone A.

Spatial Affiliations of Males

To be listed as an affiliate in a perch zone, a male had to have displayed in that perch zone with another male. Male display related to courtship comprised three categories: (1) unison "toledo" calls, (2) dances for a female, and (3) dances, sometimes involving as many as six males, in the absence of any female. Figure 3 shows the affiliation structure of just two of the six major perch zones during 1983–1986. Note that the dashed lines tend to radiate from one male, the alpha, to the beta male and perhaps to one or two other regulars. The vertical ordering of males does not attempt to reflect the dominance lineage. In K in 1985, the alpha male disappeared partway through the season; the lines therefore radiate from two males.

The number of affiliated males in the six major perch zones averaged 7.1 in any particular year ($N = 21$ zone-years; SD, 3.4; range, 3–15). Because each perch zone is attended by a cluster of males, I consider a perch zone synonymous with a lek arena (Bradbury 1981); although smaller than the leks of a number of species of grouse (Wittenberger 1978) or the unusually large leks of white-bearded manakins (*Manacus manacus*) in Trinidad (Lill 1974), these leks include more males than those of mainland white-bearded manakins (Olson and McDowell 1983) and golden-headed manakins (*Pipra erythrocephala*; Lill 1976) and only a few less than a lek of band-tailed manakins (*P. fasciicauda*; Robbins 1985). Large areas of apparently suitable habitat were rarely or never used for male display. Dance perches (fig. 1) not included in the dashed or solid lines delimiting perch zones had sporadic attendance and no male that could be clearly considered an alpha male. Perches where displays were seen fewer than four times and where female visits were never recorded were omitted from figure 1.

Most of the 55 banded males that attended perch zones from 1983 to 1986 were

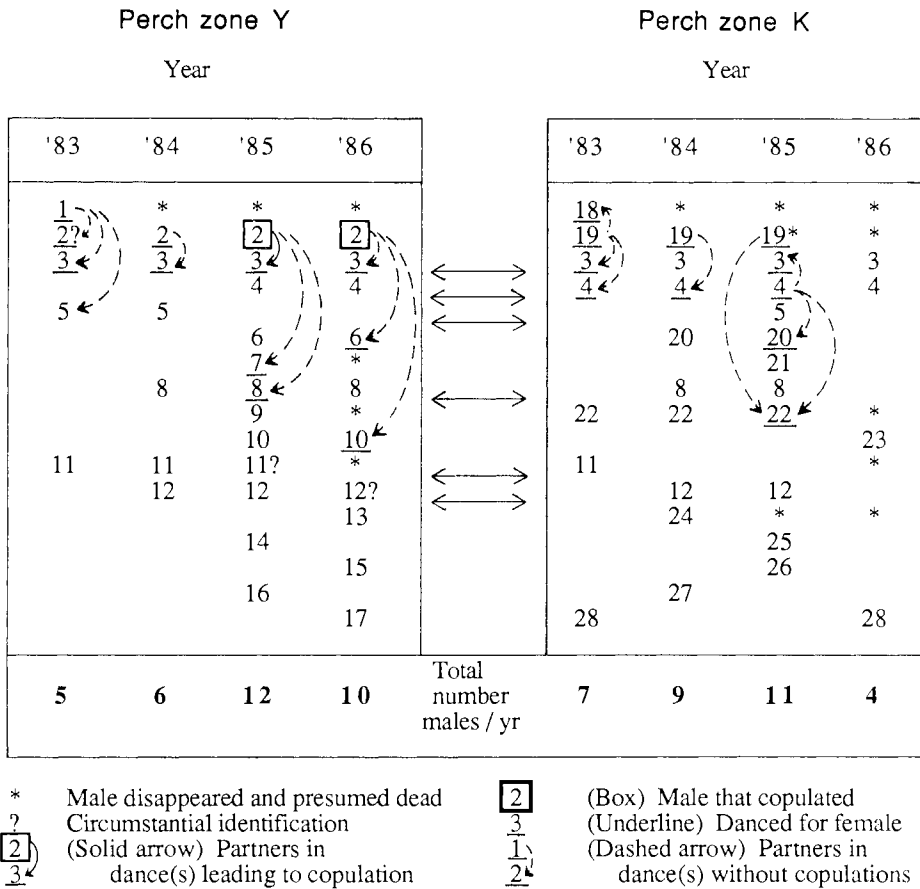Perch zone Y

Year

Perch zone K

Year

FIG. 3.—Constituencies of perch zones Y and K from 1983 to 1986. Males are identified by numbers that are unrelated to the numbers in table 1. Horizontally, therefore, the chart follows a male through time. Vertically, the chart shows the number of affiliates in a zone in a given year, with the total number at the bottom of each column. The arrows showing combinations of males that danced for females point from the dominant male (usually the alpha) to the beta or lower-ranking male. The solid, double-headed arrows between boxes for each zone link records for males that were affiliates of both zones.

affiliates in two or more zones, some in as many as six zones. Males of greater age and status associated with fewer zones (fig. 4). Younger males tended to be seen infrequently (1–10 observation periods per season), with the sightings distributed over a number of perch zones. Older males were seen more frequently (5–80 observation periods per season) but in fewer zones. An exception to the general rule of multiple-perch-zone affiliations for males was alpha males, particularly those successful in copulating. In 4 yr and over 2400 h of formal observation, only one alpha male displayed or was even sighted in a perch zone other than his primary zone.

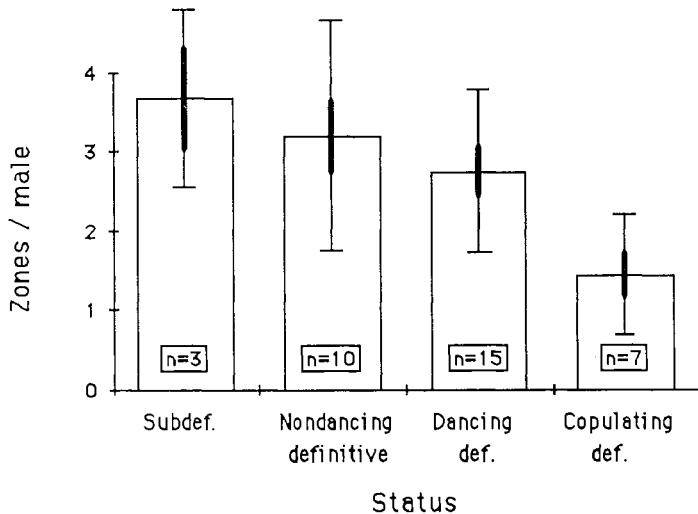No pair-wise combination of the six major perch zones in the study area had

FIG. 4.—Number of perch zones in which males of different statuses were affiliates. Bars show standard deviation (thin bar) and standard error (thick bar). Categories are the same as those for breeding-season males in figure 2.

completely nonoverlapping constituencies (fig. 5). The mean number of males shared by any two of the six major perch zones was 3.9 (N = 15 possible pairs; SD, 2.7, range, 1–9). Adjacent perch zones tended to share a higher number and proportion of affiliates (fig. 6). Each zone, therefore, was a sort of hub, in which non-alpha males with different affiliations around the rim came into contact. From figure 6, it appears that the radius of the "wheel" of male sharing around each perch zone was as much as 850 m. Because males could have different sets of interactions in the different zones, it is also of interest to ask with how many males a male interacted. Males in definitive plumage that were sighted 10 or more times (N = 32) displayed with 6.6 other banded males (SD, 4.0; median, 5; range, 2–18) during the course of the study.

Individual cases are illustrative. Male number 5 in figure 3 was noted only in perch zone Y in 1983 and 1984, in zone K in 1985, and in zone F (one of the minor zones) in 1986. This sort of serial affiliation in space and time was not atypical. Despite changing spatial affiliation, this male interacted with several of the same males in the successive perch zones. Males number 8 (hatched in 1981) and 12 (hatched in 1982) were seen together in four different perch zones in 1985. They did not display together, and one instance of a brief chase of the younger by the older male was recorded. Each, however, displayed with other older males, including the beta male in perch zone Y (number 3 in fig. 3; hatched in 1979 or earlier). This beta male displayed with at least 18 different banded males during the course of the study. In 1985, he danced for females in Y, T, and K, with three different alpha males. Of his sightings, 73% were in perch zone Y, 23% in zone T, and 4% in zone K. He appeared to hold beta status in Y, gamma status in T, and an indeterminate status (gamma or lower) in K. This male was unusual only in still
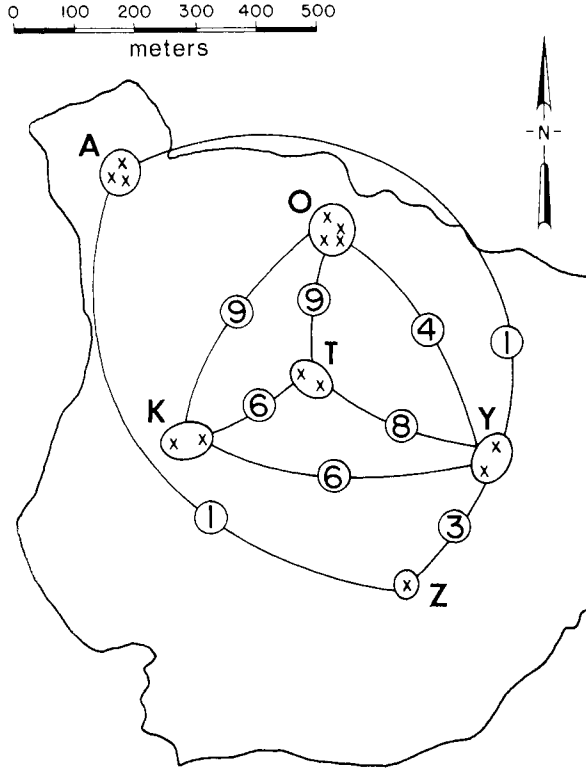
FIG. 5.—Diagram of the study area. Circled numbers indicate the number of males that were joint affiliates of pair-wise combinations of perch zones. For visual simplicity, only 9 of the 15 possible combinations are shown.
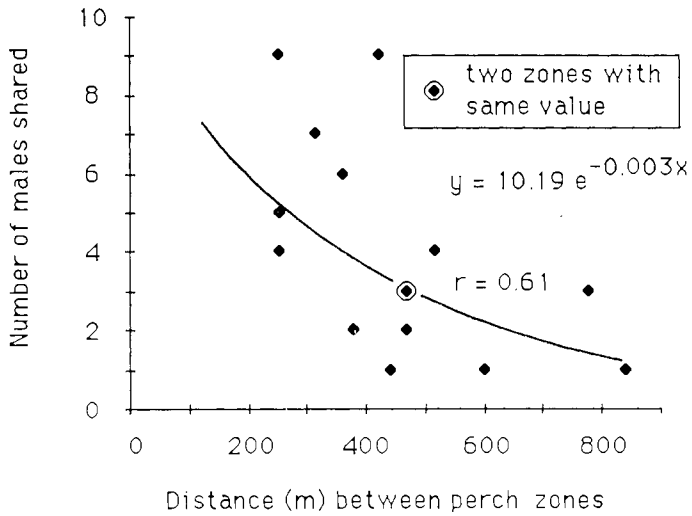

FIG. 6.—Relationship between the distances between pairs of perch zones and the number of males jointly affiliated with the two zones. The curve is the best fit to the exponential function shown.

maintaining affiliations in three perch zones after having reached beta status in a zone that received numerous female visits. Thus, males that eventually become partners probably have years of previous interactions with each other in one or more different perch zones.

Male calling effort was not confined to the six major perch zones. These were, however, the only zones with consistent levels of performance (coefficient of variation < 115% vs. c.v. > 140%) throughout a season during the 2 yr of intensive coverage. In some cases, combinations of males called at high rates for brief periods (2–6 wk). In one case, a new perch zone, C, arose that may remain stable in future years. Perch zone C showed elevated rates ($\bar{x} = 499$, $N = 4$) of "toledo" calling toward the close of the 1985 season. Calling rates remained relatively high in 1986 ($\bar{x} = 272$, $N = 24$), and the alpha male (the only unbanded alpha male in the study area) copulated once in 1986. The beta male, the oldest known-age bird in the study area, was 8 yr old in 1986 and had a previous history as an affiliate in perch zones K and O.

Spatial Scale of Patterns of Male Mating Success

Although intensive observation occurred only in the 80-ha study area, casual observations indicated that no highly successful males were present in zones adjacent to the study area. Highly successful perch zones could be identified by persistent, high rates of dual-male calling. Thus, I could estimate male performance, via casual monitoring of male calling, over an area much larger than my study area. Two such high-performance perch zones were known outside the study area. The first was 1.5 km north-northeast of perch zone Z, the most successful zone in the study area, and had a banded alpha male known to have copulated frequently in four consecutive years, from 1982 to 1985 (pers. obs.; R. Law, R. LaVal, pers. comm.). The second was 750 m west of perch zone Z. Judging from persistent calling and casual observations of dances for females, the alpha male in this perch zone may have been highly successful in copulations in both 1985 and 1986 (B. Guindon, pers. comm.). These observations place highly successful zones at a mean distance of 1.1 km from each other.

DISCUSSION

I found a fluid and complex network of interactions among male long-tailed manakins. The fluidity was pronounced among younger, especially subdefinitive, males but centered around spatially fixed alpha males that had undisputed access to females mating in their primary perch zones. The preliminary data on the age structure of male affiliates in leks and the ascent to partner status suggest that alpha and beta males are at least 8 yr of age. Only a few high-ranking males were successful in copulating. Long life spans, high survival rates, and a lack of opportunities for present reproductive success lead to the prediction that young males should delay reproduction and undertake long-term strategies that enhance future reproductive success. Such evolutionary strategies include a delay in plumage maturation and behaviors directed toward establishing a future alpha-beta partnership. The life-history schedules of males and females could scarcely

be more different. Females probably attempt one to several nestings a year throughout a long life, whereas male reproduction is concentrated in a relatively brief period at the end of the life cycle. Delayed reproduction should be favored when population size is stable (Wiley 1974). The constraint of low nesting success for females, however, may produce overriding selection for continual low investment effort that maximizes the probability of at least one successful clutch (Rubenstein 1982).

Variance of Male Copulatory Success

My results on copulatory success indicated that only one male in 55 was a top alpha in 1985. In a sample of 60 males in definitive plumage, Foster (1987) found one outlier with a testis volume greater than 100 mm^3. Interspecifically, large testis size is correlated with fertilization frequency (number of mates) in sandpipers (Cartar 1985). Together with the datum in this study for a known partner with a testis volume three standard deviations above the mean for Foster's study, these results suggest that (1) the upper range of testis volumes (≥ 75 mm^3) may always, and only, occur among the top alpha and perhaps beta males (≥ 9 yr old) and that (2) only top partners have the opportunity and capability for repeated copulations.

The variance of male mating success is the extreme yet reported for birds, both within seasons (cf. $I_S = 6.64$ for the Guianan cock-of-the-rock, *Rupicola rupicola*; Trail 1985) and over a 4-yr span. Although copulatory success does not necessarily equal reproductive success (Howard 1979), the high variance observed in this case implies that the alpha male in perch zone Z also had high reproductive success. Sperm competition seems unlikely, given a lack of evidence for multiple-zone copulations and evidence for zero copulations by the great majority of males. If sperm competition did occur, however, it would affect only the distribution of success among the few males that copulated. Clearly, males that do not copulate cannot attain direct reproductive success or engage in sperm competition.

Male-Male Interactions, Dominance, and Weight Loss

Male-male interactions (intrasexual selection) limited the "eligibility" for female visits to the subset of 6–8 alpha males and their partners among approximately 55 males in the study area in any particular season. With two exceptions, the only males seen copulating were alphas. A perch zone depends, by definition, on the presence of an alpha male; in each perch zone, the alpha male has a partner or partners with which he performs high levels of dual-male "toledo" calling (75–300 "toledos" per hour). My reliance on sampling in active perch zones with discernible alpha males may to some extent have underemphasized the fluidity, in space and time, of the associations among younger males. Transient associations were likely to pass unrecorded. The rise of a new, successful alpha male in perch zone C, in a location other than one of the traditional perch zones, suggests that the establishment of a high-performance partnership, rather than status at a particular location, may be the key to success. Because the beta male was 8 yr old, the alpha male (unbanded and of unknown age) was probably older. De novo establishment may, therefore, be simply an alternative route, not a shortcut, to attaining mating success.

The fluidity of male alliances for lower-ranking males was not readily apparent without intensive, long-term study of marked individuals. Lower-ranking males sometimes appeared only rarely at dance perches, and hundreds of hours of observation were needed to ascertain the relative status and apportionment of effort of a male such as the beta in perch zone Y. The difficulty of demonstrating fluid male affiliations may partly explain the differences in the description of male social organization between the present study and the studies of Foster (1977, 1983) in the lowlands of northwestern Costa Rica. Foster described smaller group size and did not observe multiple affiliations. Habitat differences between the drought-deciduous forest of her study and the moist forest of this study might also produce differences in social structure.

What factors influence the balance between the importance of intra- and intersexual selection? Weight loss during the breeding season has been demonstrated for a number of species in which sexual selection is important (Robinson 1986). The age-graded weight loss presented here differs from that demonstrated by Robinson for yellow-rumped caciques (*Cacicus cela*) in that older, lighter males did not lose dominance status. Instead, a correlation existed between the extent of courtship display and weight loss. The extent of courtship display, in turn, correlated with male success in obtaining female visits and copulations (McDonald 1989). Broad patterns of age-graded dominance across cohorts might hide more-subtle patterns within cohorts. For example, one might expect that within cohorts the establishment or maintenance of dominance would correlate positively with weight. The existing data are insufficient to test this hypothesis.

In contrast to the swallow-tailed manakin, the congeneric long-tailed manakin has a longer delay in plumage maturation and less disruption of courtship display (Foster 1983). Enforcement of an orderly age-graded dominance queue may be explained by the tendency of females to leave dance perches at which overt agonism occurred among males. Intrasexual selection within a lek is thus reinforced by intersexual selection among leks. For orderly age-graded queuing to be favored, long-term, stable relationships among males are required as well as either (1) high survival rates to overcome the discount on delayed versus immediate benefits or (2) indirect selection that promotes reproductive restraint. If survival rates are lower in swallow-tailed manakins, less stable relationships in leks and a lower probability of obtaining delayed benefits may favor higher levels of attempted disruption. The shorter delay in plumage maturation in swallow-tailed manakins (Foster 1987) supports such a life-history-based interpretation.

Delayed Plumage Maturation

The results of this study do not support the hypothesis that subdefinitive males mimic females in order to gain immediate copulations (Rohwer et al. 1980) (1) because subdefinitive plumages, especially the plumages 2 and 3 yr after hatching, were distinct from female plumages and (2) because direct observation suggested that subdefinitive males (and many definitive males) rarely or never display for females, much less copulate. Furthermore, Foster's (1987) data on the small testis volumes of subdefinitive males and the pronounced grading of testis size by age suggest few prospects for copulations by subdefinitive males.

The results also fail to support entirely the juvenile-mimicry hypothesis of Foster (1987). The word mimicry implies deception. Foster's hypothesis suggested that, in part, later subdefinitive plumages deceptively mimic those of pre-reproductive immature males that are incapable of fertilization. Established males, deceived by the apparently immature plumages, would allow access to copulations with females. Two points provide evidence against this hypothesis. First, sharply graded subdefinitive plumages clearly distinguish "immature" males (≤1 yr old) from older subdefinitive males in dark-face or blue-back plumages. The plumage stages described here are more distinct from each other and thus provide less opportunity for deceptive mimicry than do those suggested by Foster (1987). Foster proposed that red-cap and dark-face plumages represent the same age class (1 yr after hatching) and that the blue-back-plumage stage lasts 2 yr (2 and 3 yr after hatching). The second evidence is that even definitive males of age 4–7 yr appeared to be little threat to the prerogative of alpha males in gaining access to females. Males in any plumage state were tolerated in the perch zone except during female visits, when both subdefinitive and definitive males were chased by the alpha or beta male or both. Furthermore, rates of intrusion by either subdefinitive or definitive males during female visits were low and did not appear to affect copulatory success. Point 2 against the female-mimicry hypothesis also argues against the juvenile-mimicry hypothesis, although rare opportunities for copulation might exist that were overlooked.

Cohort Signaling

The subdefinitive plumages vary at two levels. First, year classes differ from each other in a marked, discernible manner: from red cap to dark face to blue back to definitive. Second, within the subdefinitive age classes, males differ more subtly in progress toward the definitive plumage. Such differences involve fullness of the red cap in the year after hatching, degree of blackening 2 yr after hatching, and both darkening and extent of blue feathering 3 yr after hatching. Both levels of variation require an explanation. A crucial question is whether the subdefinitive plumages act as signals and, if so, which individuals are the targets of the signal. At the level of broad differences among age classes, I propose that the subdefinitive plumages function primarily as honest signals of status (Lyon and Montgomerie 1986). Status, in this context, can be equated with age. The signal is honest insofar as it accurately indicates the age class, and therefore status, of the subdefinitive males. Both the female- and juvenile-mimicry hypotheses, outlined above, suggest that the signal is deceptive and that it is aimed at top partners in each lek. The cohort-signal hypothesis, however, suggests that the plumages are directed primarily at males in a male's own cohort or in neighboring cohorts. A secondary function of the subdefinitive plumages, suggested also by Foster (1987), would be to promote a tolerance of young males by older males during a period of establishment within a lek. Both the female-mimicry hypothesis and the juvenile-mimicry hypothesis posit present reproductive gains as a benefit from delayed plumage maturation. The cohort-signal hypothesis proposes little or no immediate reproductive benefit from the transitional plumages. By adopting transitional plumages that act as indicators of age and status, males of widely disparate ages,

with dissimilar reproductive interests, avoid unnecessary conflict, whereas males of similar age recognize potential competitors for age-specific roles. This hypothesis is consistent with the observation that overt aggression, when seen, tended to occur between younger, unestablished males of similar ages, such as the 3- and 4-yr-old males, number 8 and number 12 (fig. 3; perch zone K in 1985). Such agonism occurred during male-only displays, such as the popcorn hops. Within subdefinitive age classes, variability in plumage might serve either (1) to facilitate individual recognition among individuals that have not interacted over a period long enough to allow recognition on the basis of vocalizations or behaviors or (2) to reflect condition, such that birds with a greater development of definitive plumage elements (red, black, or blue) would be signaling superior condition. The results of the present study do not allow discrimination among these alternatives.

Given the low prospects for immediate success even for males in early definitive stages (4–7 yr of age), the question changes from why males delay maturation for four years to why they do not delay longer. If individual recognition occurs, a male, once recognized by vocalizations or behavior, would no longer need a plumage badge (Rohwer 1982) to indicate his status. Such recognition may occur only when males spend relatively more time in fewer perch zones (fig. 2). Adoption of the definitive plumage might then be favored by rare opportunities for display to females or as a general signal, directed at younger males, of status as an established affiliate.

An alternative hypothesis for delayed plumage maturation, not involving a signal function, would be that subdefinitive plumages represent a response to costs (via predation or energetics) of producing showy definitive plumage (Selander 1972). In contrast to a study of the Guianan cock-of-the-rock by Trail (1987), no predation attempts on displaying males were seen during almost 2500 h of observation. Although no predators are now apparent, the habitat does not lack any obvious potential predators that might have been important in past selection, and observations from more-typical lowland habitats do not suggest a striking difference in predation pressure there (pers. obs.; Foster 1977). Thus, predation seems unlikely to have been a primary selective force behind delayed plumage maturation in long-tailed manakins. Females, with no showy plumes, bear the cost of egg and nestling production and therefore may not be useful as a standard against which to assess the energetic costs of the definitive male plumage. Although the long life spans and high survival rates of definitively plumaged males suggest that the plumage is not extremely expensive energetically, such cost would have to be assessed against a hypothetical male not assuming the definitive plumage.

Costs and Benefits of Cooperation

It seems unlikely that the eventual partnerships represent differential associations of kin. Partners appear to differ considerably in age, making sibship unlikely. The multiple affiliations of males mean that a male's eventual partnership role may result from unpredictable changes in rank in the leks with which he is affiliated. Relatedness to each of several potential partners in the different leks seems unlikely to be greater than the relatedness to a randomly chosen male in the local

population. Thus, the cooperative behavior of the beta male may be more par-simoniously ascribed to individual strategic considerations than to indirect selec-tion. The high variance of male copulatory success means that reproductive opportunities for young males were virtually nonexistent. Two potential direct benefits of cooperation by the beta male are apparent from the results. (1) The beta male has rare immediate opportunities for copulations. In a species with such high variance, even rare copulations at an age (8–10 yr) when most males never copulate could be important. (2) The beta male gains a delayed benefit via ascent to alpha status upon the disappearance of the preceding alpha male. If beta males generally ascend to the alpha role and if females tend to return to where they have mated previously, then a beta male establishes his own future success by enhanc-ing that of his alpha. Certain alpha males gained clear immediate benefits from the cooperation of beta males, in the form of copulations. Elsewhere (McDonald 1989), I have shown that an alpha male had lower mating success after his beta male partner disappeared and was replaced by the gamma male. I also provided evidence that females did return to leks after the disappearance of the preceding alpha. The contribution of indirect selection to the evolution of cooperation could, however, be more rigorously tested by DNA fingerprinting (Burke and Bruford 1987) or other genetic analyses.

In conclusion, changes in male behaviors, weights, and testis volumes with increasing age may be responses to the high variance of mating success. Domi-nance status was not affected by weight loss. The results are consistent with the hypothesis that subdefinitive plumage is an honest signal of age-based status. Such signaling may function in age-graded queuing for future positions in leks. Given the present levels of the variance of mating success, present and future direct benefits to cooperators in the face of extremely limited prospects for reproductive success may be sufficient to explain the maintenance of male-male cooperation. Whether high variance preceded cooperation and acted as a driving force in its evolution and the evolution of the age-graded changes in behavior and morphology may best be addressed by comparative studies of other species of manakins (Pipridae).

SUMMARY

Long-tailed manakins, *Chiroxiphia linearis*, are birds with a lek mating system and male-male cooperation in courtship display. I studied male-male networks in a color-banded population in Monteverde, Costa Rica, from 1981 to 1987. Males displayed in scattered leks (75–300 m apart) comprising 3–15 males. Within each lek, an alpha and beta male, with strict relative dominance ranks, performed most of the courtship display. Of 50–60 active males per season, only 6–8 males were well-established alpha males in leks with consistent levels of dual-male displays (calls and dances). Demographic data suggest that males may be 8 yr of age or more before attaining beta status. Alpha tenure can last from two to at least four years.

Alpha males were rarely or never seen in perch zones other than their primary perch zone (their area of dominance). Lower-ranking males maintained simultane-

ous affiliations with males in as many as six different zones. Each zone, therefore, acted as a hub in which males with different affiliations around the rim came into contact. Each of the six major perch zones shared at least one affiliate with each of the other zones, and roughly half the males in any particular zone were also known affiliates in one or more other zones. Marked changes occurred in male traits with increasing age and status: (1) significant declines in weight throughout the life span, without loss of dominance status; (2) a 4-yr delay in plumage maturation with distinct subdefinitive, transitional stages; (3) reduction in the number of perch zones with which older males maintained affiliations; and (4) increasing probability of copulatory success. The results are consistent with the hypothesis that subdefinitive plumages in this species serve primarily as accurate indicators of age, which in turn largely determines status, and that males queue for positions in an age-based dominance system. The results do not support the hypothesis that delayed plumage maturation involves mimicry or deceptive signaling by subdefinitive males (≤ 3 yr old) to high-ranking males (≥ 8 yr old).

Of 85 males monitored from 1983 to 1986, copulations ($N = 117$) were distributed among 8 males. Four of these males accounted for over 90% of the copulations, with 67% accruing to one male. An index of the opportunity for sexual selection, to be used cautiously in interspecific comparisons, was estimated to range from 15.8 to 31.5 in four successive years. Direct benefits to cooperation by the beta male consisted of rare immediate copulations ($N = 2$) and eventual ascent to alpha status ($N = 3$). The high variance of mating success means few opportunities for success by younger males and should favor long-term strategies, such as cooperation and delayed plumage maturation, that enhance the prospects of future success.

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