

Correlates of male mating success in a lekking bird with male-male cooperation

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Abstract. Correlates of male mating success were examined in a population of long-tailed manakins, *Chiroxiphia linearis*, that included 270 colour-banded individuals. Long-tailed manakins have a lek mating system and male-male cooperation in courtship display. Multivariate analysis of behavioural variables indicated that female visitation correlated with the number of unison 'toledo' calls given by male partners. Given a female visit, copulatory success was correlated with the 'butterfly' display component of the dual-male dance. Both 'toledo' output and dance display differed significantly between perch-zones. Only six to eight partnerships in a local population of as many as 55 males per season performed call displays at a level (75-335 toledos per h) that was correlated with any female visitation. Data on crown plumage of female visitors suggested that younger females may have been less discriminating than were older females. The relationship between variance in mating success and the evolution of cooperative male display is discussed.

In lek mating systems male-male competition (intrasexual selection) or female choice, or both, could affect male mating success. Variance in male mating success may be the single most important component of fitness in such systems. Although high variance in mating success has long been noted for many lek species (Lill 1974; Bradbury 1981), efforts to determine correlates of male success have been less successful. Recently, greater intensity and quantification of behavioural sampling, use of multivariate statistical analysis, and theoretical insights have led both to success in describing correlates and revision of earlier conclusions regarding patterns of success in certain species (Gibson & Bradbury 1985). Gibson & Bradbury's study implicated male performance of courtship displays in sage grouse, *Urophasianus centrocerus*, as a correlate of mating success.

Although lek species are widely distributed in habitat, geography and taxonomy, they tend to be relatively rare within a taxon. Two interesting exceptions to this rule are the avian families Paradisaedidae (birds-of-paradise) and Pipridae (manakins). In these two families of frugivorous

birds, the former Old World and the latter New World, lek mating is the rule. Lek mating is perhaps the clearest example of sexual selection and is characterized by intense competition between males. It seems paradoxical, therefore, to find that in one genus of manakins, *Chiroxiphia*, males cooperate in courtship display (Foster 1977, 1981). Incipient cooperation has been reported in two species of the manakin genus *Pipra* (Schwartz & Snow 1978; Robbins 1985), possibly in birds-of-paradise (LeCroy et al. 1981), and in wild turkeys, *Meleagris gallopavo* (Watts & Stokes 1974; Balph & Balph 1980). In the genus *Chiroxiphia* two or more males form teams that may persist for several years (Snow 1971; Foster 1977, 1981). Partnered display raises the possibility that female choice, if it occurs, is based upon the combined characteristics of team members. Thus, intersexual selection could shape intrasexual selection and the formation of male teams. I have examined the composition of the spatially and temporally fluid teams in the long-tailed manakin, *Chiroxiphia linearis* (McDonald, in press). I found that only a small subset of males actually performs courtship displays for females. An extended period of male-male interactions appears to predetermine the access of older males (greater than 8 years of age) within a team to any

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females that watch dance displays. In this paper I examine the correlates of male mating success, with particular emphasis on aspects of dual-male performance of courtship displays.

NATURAL HISTORY AND STUDY POPULATION

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 1300 m. I colour-banded 270 long-tailed manakins in the study area between 1981 and 1987. Of these, 69 were known to be females, either because they had vascularized brood patches (males also have an abdominal apterium), because they remained in green plumage for more than one season, or because they exhibited female-like behaviour 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. Between 1983 and 1987, 59 banded males displayed at and 30 banded females visited perch-zones in the study area.

For courtship display adult males formed teams, with an alpha and beta core pair and 1-11 auxiliary affiliates ($\bar{X} \pm \text{SD} = 7.1 \pm 3.4$, $N = 21$ perch-zone years). For much of each day throughout the breeding season two males, usually the alpha and beta, but occasionally other combinations of male affiliates, give an advertising call in unison from the subcanopy. This call phonetically resembles the word toledo. Upon the arrival of a female, all three move to the dance-perch, a horizontal branch or vine within 1.5 m of the ground. The males then perform a dance bout comprising sets of backwards leapfrog hops alternating with laboured butterfly flight. During butterfly flights the males move as much as 20 m away from the perch, returning to the perch simultaneously or sequentially at intervals of a few seconds. After two to eight sets of hops (usually 20-40 hops per set) and two to eight butterfly displays (usually 10-50 s per display), the beta male leaves the immediate area of the dance-perch and the alpha male continues with a solo butterfly display for 1-8 min. If the female is receptive, the alpha male performs a rapid ending

flight followed by copulation on the dance-perch. Even when more than one female attended a dance, only one female copulated. I have no evidence for non-perch copulations. Neither dance hops for females nor toledo bouts (greater than eight toledos) were ever performed by a lone bird. In those cases where an alpha male disappeared and was replaced by a banded bird, the new alpha had previously been the beta ($N = 3$).

METHODS

I banded males and females with individual combinations of coloured plastic bands from A.C. Hughes, Ltd., England. Perch-zones were defined as the area (less than 3 ha) in which a particular alpha male was dominant. Sampling effort concentrated on six major perch-zones (Fig. 1) upon which the bulk of the results from 1983 to 1987 are based. Eight other perch-zones, sampled less intensively during the 5-year period, had sporadic activity levels and most received few, if any, female visits. I erected blinds at 22 dance-perches of males (eight major and 14 minor perches) in the study area. Blinds were 8-12 m from the dance-perch. When possible, blinds were placed at an oblique angle to the axis of the perch, so as to avoid interference with the path of butterfly display. The basic sample unit was a 2-h period of observation from a blind. The dual-male toledo calls were counted and 22 variables describing male and female attendance and behaviour were recorded. Every fifth minute during a 2-h observation was a sample block during which certain counts were conducted. Males vocalize with each hop during dances. Thus, stereo recordings of observers' voice notes, overlying male calls, allowed timing of the temporal sequence of male dance displays. When possible, simultaneous observations by two-six observers took place at two or more different perch-zones (83% of observations). The movements of five different females were monitored with 2-g radio transmitters from Custom Electronics, Urbana, Illinois. Transmitters were attached to the feathers of the dorsum with polyacrylate glue.

Analysis of Data on Visitation and Copulatory Success

I used one dependent and 11 independent variables for analysis of data on female visitation (Table 1). For the 1984 data, I omitted the variables

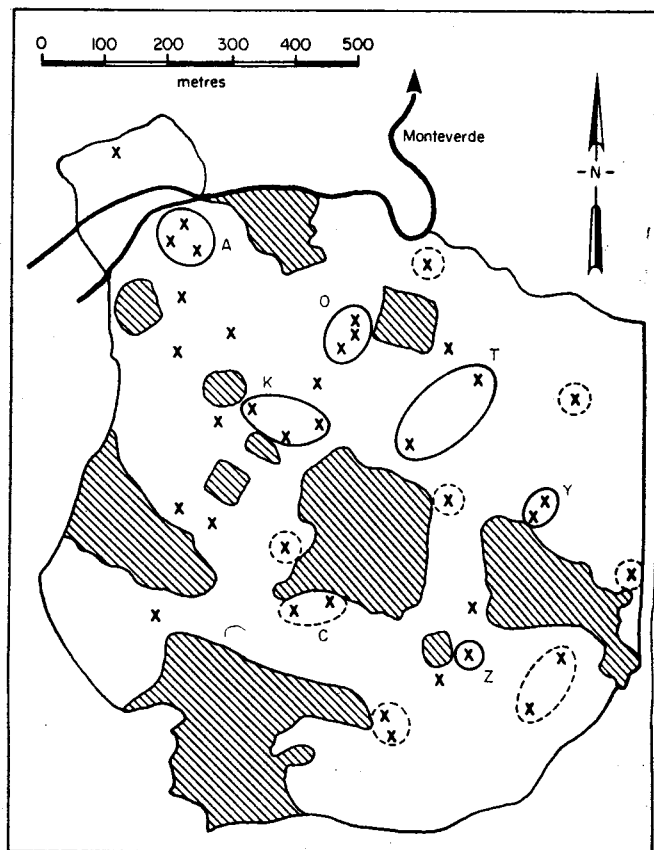


Figure 1. Diagram of study area in Monteverde, Costa Rica, for study of long-tailed manakins, 1981-1987. Solid circles, with alphabetical labels: six major perch-zones; dashed circles: minor perch-zones; hatching: pasture.

Gap, Bouts and Residuals because of large numbers of missing values.

Because many of the independent variables were correlated, I used principal components analysis to reduce the number of variables. Few of the variables were normally distributed, even after Box-Cox transform procedures (Sokal & Rohlf 1981). I therefore used a non-parametric multivariate analysis of variance (Zwick 1985). Essentially, the test performs a multivariate analysis of variance on a ranked data matrix. If the overall test statistic (t_s)

is significant, one can ask whether particular variables make a significant contribution to the overall difference between groups (Katz & McSweeney 1980). The test statistic is the difference in mean ranks between groups. This value is contrasted with a critical value computed from the sample sizes of the contrasted groups and a Bonferroni chi-squared statistic (see Table 22 in Kres 1983).

I used one dependent and three independent variables for analysis of data on copulatory success

Table III. Comparison of observations with and without female visits, on the basis of principal components analysis

Year	Category	N	PC1	PC2	PC3
1984	Visit	45	162.0	83.5	72.0
	No visit	190	107.6	126.2	128.9
	Difference between groups		54.5*	-42.7*	-56.8*
1985	Visit	123	337.5	215.7	198.8
	No visit	340	193.8	237.9	244.0
	Difference between groups		143.7*	-22.2	-45.2*

Scores are mean ranks for the three principal components ($df=1$). Sample size is the number of 2-h observations.

* $P < 0.005$.

contributed significantly to group differences (Table III).

Loadings on principal components should be interpreted cautiously, since one is looking at the data in only one dimension. For the 1985 data, the three highest positive loadings on PC1 (45% of the variance explained) were Bouts, Toledos and 2 (two males attending). PC1 loaded negatively on Gap and on the highly correlated measure 0 (zero males attending). PC1 therefore appeared to measure dual-male attendance and calling effort. PC3 (16% of the variance) loaded negatively on Toledos, and was negatively correlated with the dependent variable, Visitation. It loaded strongly positively on 'Teeamoos' and 1 (one male attending). PC3, therefore, appeared to reflect lack of response, by a beta male, to his alpha male's attendance and teeamoos. The interpretation of the 1984 loadings is similar. PC2 (17% of the variance) loaded positively on Extra (more than two males sighted during the observation), 3 and Residuals. It loaded negatively on Teeamoos and 1. PC2 appeared to measure male-only dances and multiple-male interactions that were uncorrelated (1985) or negatively correlated (1984) with Visitation. Thus, two aspects of male performance, Toledos and 2, correlated positively and consistently with female visitation.

Differences between zones

Given that visitation was correlated with dual-male performance, it is of interest to ask whether performance differed between zones. Female visitation rates at perch-zones accorded well with the

seasonal mean for toledo counts at the six major perch-zones in both 1984 and 1985 (Fig. 2). Figure 3 depicts the difference between perch-zones for the performance characteristics correlated with visitation in the principal components analysis. Each zone's deviation from the mean rank is plotted for PC1 and PC3. As noted above, in both years PC1 and PC3 contributed significantly to the difference between observations with and without female visits. In both years, Z was the only perch-zone whose values lay in the same quadrant (+ for PC1, - for PC3) as that for the visited group (Vis). Overall, heterogeneity between perch-zones was significant in both 1984 ($N=235$ 2-h observations, $t_s=133.6$ $df=15$, $P<0.01$) and 1985 ($N=463$, $t_s=251.7$, $df=15$, $P<0.01$). Significant differences existed between perch-zones for PC1 and PC3 in both years (Table IV). Thus, perch-zones did differ in performance and these differences correlated with differences in female visitation.

Opportunity for Females to Sample Males

Data from mist-netting, resighting, and limited radiotracking indicated that females ranged widely, both within and between seasons. I resighted or recaptured 44 females. The maximum distance between resightings or recaptures for each of 23 of these females was more than 300 m. The maximum distance for each of 14 of the females was more than 500 m, including two distances greater than 1 km. Since I netted and observed infrequently outside the study area, the maximum may have been limited more by observer effort than by the movements of the birds. On four occasions, females were recaptured or resighted at locations more than 700 m apart, within the space of six days. A banded female that lost a nest with eggs copulated a week later 750 m away at Perch-zone Z. To do so she had to pass through the perch-zones of at least five other male teams. I estimate that the home ranges of females were as large as 80 ha. Thus, females should have the opportunity for auditory comparison of all, or nearly all, the zones within the study area.

Only one banded female was seen to visit more than one zone within a season, but indirect evidence indicated multiple-zone visits. The most successful perch-zones obtained a higher proportion of copulations than of visits (e.g. 46% of visit, 75% of copulations at Perch-zone Z in 1985). Thus, some females that visited other zones probably

Table I. Variables for analysis of data on female visitation during 2-h observations

Variable	Definition
Independent	
Display	The number of displays on the dance-perch involving only males
Extra	The number of extra males observed, in excess of two partners (alpha and beta)
'Teeamoo's'	The teeamoo call appears to function in male-male communication, as a partner attractant. The value is based on the number of sample blocks in which a teeamoo call was heard. Values could range from 0 to 24
0, 1, 2, 3	The number of sample blocks during which exactly zero, one or two males, or three or more males was heard or seen in the vicinity of the dance perch
Bouts	The number of bouts of toledo calls during an observation. A bout was defined as a sequence of toledos with no pause greater than 30 s
Gap	The number of gap minutes during which males were neither giving toledo calls nor dancing for a female
'Toledos'	Adjusted toledo count. Males did not toledo while dancing. The toledo rate (per minute) during the remainder of the observation was multiplied by the duration of female visitation. This estimate was then added to the unadjusted total count of toledos
Residuals	The residuals of a regression of Bouts against Toledos, as a measure of whether toledos were delivered in long or short bouts
Dependent	
Visitation	Its value was 0 if no females visited, 1 if one or more females visited. Visitation was highly correlated with another measure of success, the number of distinguishable females visiting during an observation ($r=0.86$)
Principal components	
PC1, PC2, PC3	The first, second and third principal components derived from reduction of the 11 independent variables

Table II. Variables for analysis of data on copulatory success following dance episodes

Variable	Definition
Independent	
Toledos	Toledo count for the associated 2-h observation period (see Table I)
Hops	The mean number of hops per set during a dance bout. A dance bout was defined as all the sets of hops and butterfly flights by the males, from the time at which a female arrived in the immediate vicinity of the dance perch until she either copulated or left
Butterfly	The mean duration of dual-male butterfly flight for the sets in a dance bout. I included only butterfly flights that were unequivocally sandwiched between sets of hops, since butterfly display sometimes tapered off, without further display
Dependent copulation	Its value was 0 if no female copulated, and 1 if a female did copulate

of males (Table II). The non-parametric tests by Zwick and by Katz & McSweeney were run on the ranked data matrix.

RESULTS

Correlates of Female Visitation with Male Display

Samples pooled across perch-zones

I pooled samples from all perch-zones within

years to look for differences between observations with and without female visits. The overall difference between observations in which females visited (1984, $N=45$; 1985, $N=123$) versus those in which they did not (1984, $N=190$; 1985, $N=340$) was significant in both 1984 ($t=53.92$, $df=3$, $P<0.001$) and 1985 ($t=111.46$, $df=3$, $P<0.001$). For the 1985 data, PC1 and PC3 contributed significantly to group differences, but PC2 did not (Table III). In 1984, PC2, as well as PC1 and PC3,

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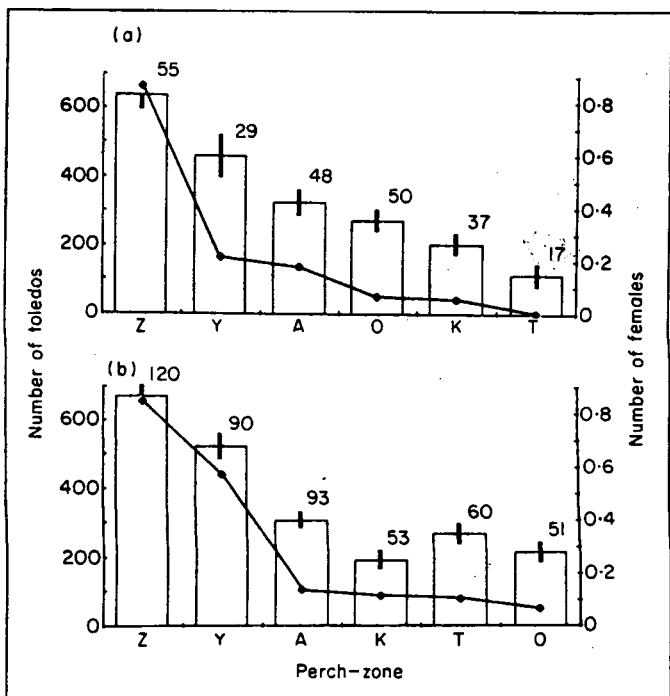


Figure 2. Number of toledo calls (bars; mean $\pm$ se) and number of female visits (line; mean) per 2-h observation at six major perch-zones in 1984 (a) and 1985 (b). Zones are arranged in decreasing order of female visitation. Sample size is number of 2-h observations at that perch-zone.

copulated at the most successful zone(s). Further, of those females that visited perch-zones, the proportion that were banded was relatively small (less than 33%), suggesting a female pool drawn, in part, from outside the study area and making it more difficult to document multiple-zone visits. In contrast, virtually all alpha and beta males and most other affiliates were colour-banded and had high resighting rates within the zone or zones at which they were affiliates.

Correlates of Copulatory Success

Between 1983 and 1986, 117 copulations were observed, all but two by alpha males. The two exceptions were copulations by the beta male of the most successful team in the temporary absence of the alpha male. Copulatory success was at least partially independent of visitation success. That is, copulations did not accrue as a simple proportion

of visits received, since differences in proportions of dances leading to copulations existed both between perch-zones within years, and between years within perch-zones. Eight of 85 males monitored between 1983 and 1986 were successful in copulating, with four of the males accounting for over 90% of the copulations during the 4-year period. The distribution of copulatory success is given elsewhere (McDonald, in press).

Behaviour of males and females

Males were never seen to follow or harass females. Females could leave at any stage of the dance, including attempted mounting following a dual-male display and solo by the alpha lasting more than 20 min. Although more than one female watched some of the dance displays (59 of 273), at most one female copulated per display ($N=32$). In some other lek species female precopulatory behaviour is relatively cryptic and involves only a

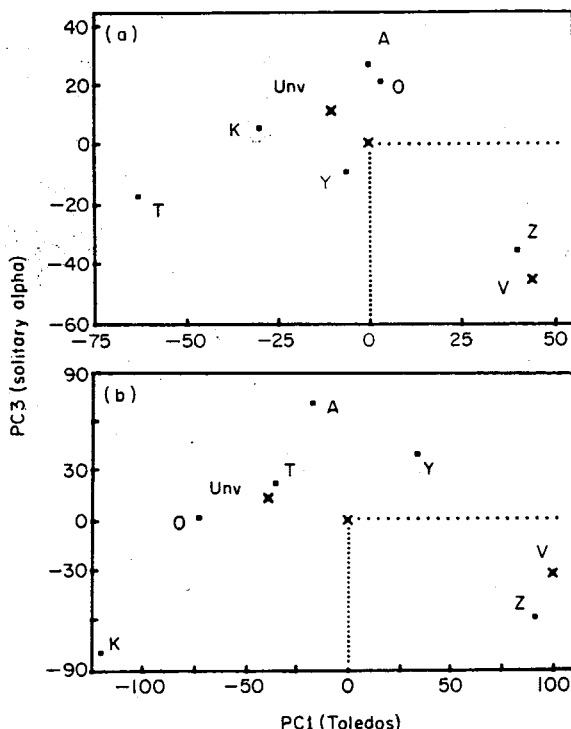


Figure 3. Scores of male display related to female visitation in (a) 1984 ($N=235$) and (b) 1985 ($N=463$). Scores are listed as the deviation from the mean ranked principal components, score, for PC1 and PC3. Each of the six major perch-zones is represented by its alphabetic name. Also plotted is the mean rank, for all zones combined, of those observations with female visits (Vis) and of those during which no female visited (Unv). Dotted lines separate the quadrant in which deviations are positive for PC1 and negative for PC3.

crouching posture, which may not be a good indicator of receptivity (e.g. Kruijt & Hogan 1967). In contrast, the precopulatory behaviour of long-tailed manakins was indicative of the probability of successful copulation. As a dance progressed, females that eventually copulated moved actively on the perch. Movements included side-to-side shuffle and upward hops with the wings held high above the back (resembling the male's wing movements immediately prior to copulation). Females often, but not invariably, followed the alpha male to his landing-spots away from the dance-perch during the solo display. Even females that were known to have copulated previously at a zone within or between seasons were seen ($N=11$) to watch a full dance display without making rapid movements, and to leave without copulating.

Measures of performance of dance displays

Figure 4 shows three measures of performance that might serve as correlates of copulatory success: Toledos, Hops and Butterfly. Excluding dances with missing values, successful (1984, $N=20$; 1985, $N=36$) and unsuccessful dances (1984, $N=16$; 1985, $N=70$) showed significant multivariate differences in both 1984 ($t=9.3$, $df=3$, $P<0.05$) and 1985 ($t=18.6$, $df=3$, $P<0.001$). In 1984, only one of the three variables, Butterfly, contributed significantly to this difference (Table V). In 1985, two of the three performance variables contributed significantly to the group difference: Toledos and Butterfly (Table V). Hops did not differ significantly between successful and unsuccessful dances in either year.

The results for the correlation between Butterfly

Table IV. Multiple comparisons of male performance between perch-zones, based upon principal components scores

Year	N	Perch-zone	Perch-zone					
			Z	O	A	Y	K	T
1984	54	Z	—	37.21	40.70	46.15	69.88**	103.15**
	50	O	56.15**	—	3.49	8.94	32.67	65.94
	48	A	61.91**	5.76	—	5.45	29.18	62.44
	29	Y	25.49	-30.66	-36.42	—	23.73	57.00
	37	K	40.30	-15.85	-21.61	14.81	—	33.27
	17	T	17.53	-38.62	-44.38	-7.96	-22.77	—
1985	117	Z	—	164.61**	109.19**	58.08	212.81**	128.33**
	51	O	59.99	—	-55.42	-106.53**	48.20	-36.28
	92	A	129.95**	69.96	—	-51.11	103.62**	19.14
	90	Y	99.30**	39.31	-30.65	—	154.73**	70.25
	53	K	-19.96	-79.95	-149.91**	-119.26**	—	-84.48
	60	T	79.59*	19.60	-50.37	-19.72	99.55*	—

PC1 differences are entered in the upper diagonals and PC3 differences in the lower diagonals. Numbers represent the difference in mean rank between the perch-zone in the row and the perch-zone in the column, for a multiple comparisons test (Katz & McSweeney 1980). Thus, for 1984 on PC1, the mean rank at Perch-zone Z minus that at Perch-zone O was 37.21 (ns). Sample size is the number of 2-h observations.

* $P < 0.05$; ** $P < 0.005$.

and Copulation are inherently conservative: short butterfly displays before copulations may reflect increased receptivity of the female due to prior exposure to long butterfly displays. For successful dances at Zone Z in 1985, six of the 10 shortest butterfly displays represented known or suspected short-term return visits by females. The earlier 'unsuccessful' dances included Butterfly 36% longer than those in all unsuccessful dances and 6% longer than those in all successful dances. The three shortest butterfly displays for successful dances were at zones other than Z. It was not known whether other dances preceded these short butterfly displays, but the females may have been young, naive choosers.

The Butterfly-Copulation correlation might arise because of a male response to female excitedness: reverse causation from the hypothesis that male performance determines female response. Females showed a decided progression of movement activity in dances preceding copulation. Females that did not become active left the perch-zone without copulating. If males responded to increasing female excitedness by increasing the duration of butterfly flights, we would expect an increase in the durations of successive butterfly flights within dance bouts leading to copulations. No such trend was evident (Table VI). This result

suggests that the duration of butterfly display (or an unmeasured, highly correlated cue) does promote copulatory receptivity in the females.

Switching between zones by females

Altogether, Perch-zone Z accounted for 83% of the copulations in 1984, and 75% of those in 1985. The new females that copulated at perch-zones other than this top zone may have been naive females with relatively undeveloped powers of discrimination. With greater experience, such females might switch preferences to top zones and then become site-, or more properly, team-faithful. Support for this hypothesis comes from the fact that 15 banded females visited perch-zones other than Z. Of these, five made switches in attendance between seasons. Of the females switching zones three females switched to perch-zone Z. Of 17 banded females that visited Perch-zone Z, only one switched to another zone, and that switch followed a drop in toledo quality in 1986-1987 (see below). Previous to that switch, four females returned in successive seasons, and five others returned, within a season, at intervals long enough to represent fertilization of a second clutch.

An independent line of evidence comes from crown plumage of banded females. Older female manakins may attain male-like plumage (personal

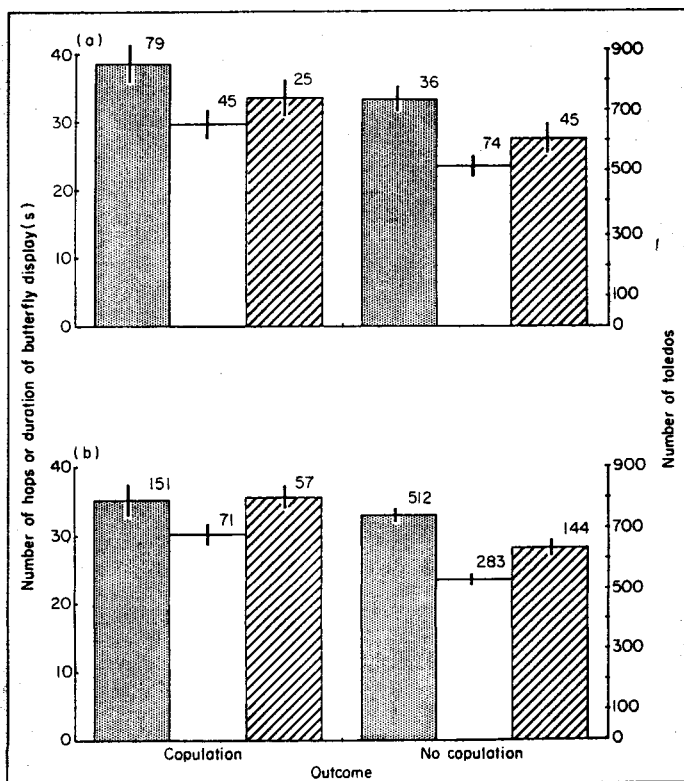


Figure 4. Measures of male dance display in successful and unsuccessful dance bouts in (a) 1984 and (b) 1985. Bars show mean $\pm$ SE for Hops (■), Butterfly (□), and Toledos (▨). The Toledo count represents the 2-h total for the observation in which the dance occurred. Sample sizes are shown above the bars and represent number of hop sets, number of butterfly displays and number of 2-h observations, respectively. The multivariate tests for dance display (Table V) were run on a subset of these data.

observation; J. Karr, personal communication). Female long-tailed manakins occasionally have reddish or tawny crown feathers. Of 53 females with adequate records taken at the time of netting, 14 (26%) had tawny crowns. Of 13 female visitants at Zone Z whose crown plumage had been noted during mist net processing, six had tawny crowns. Of 11 known-state females visiting other perches, none had a tawny crown ($\chi^2 = 4.8$, $P < 0.05$). I noted tawny crowns but did not, at first, note green crowns. Thus, the actual proportion of green females is almost certainly higher, making the test more conservative.

Lack of tradeoffs between components to success

The partners from Perch-zones Z and Y performed at the highest levels for toledo display in both 1984 and 1985 (Fig. 2). In 1985 these were the only perch-zones with positive mean deviations on PC1 (Fig. 3). Further, these two pairs danced more often, and at higher levels (as measured by total number of hops and duration of butterfly display), than males at any other perch-zone (Fig. 5). Cumulatively, these two teams received 79% of all female visits in 1984 and 78% of all female visits in 1985. For Toledos, Butterfly and Hops, the levels at Perch-zones Z and Y were significantly higher than

Table V. Comparison of dances with and without copulations, on the basis of three measures of male performance of displays

Year	Category	N	Toledos	Hops	Butterfly
1984	Copulation	20	20.6	20.6	22.7
	No copulation	16	15.9	15.9	13.3
	Difference				
	between groups		4.7	4.7	9.5*
1985	Copulation	36	66.2	56.4	67.2
	No copulation	70	46.9	52.0	46.5
	Difference				
	between groups		19.3**	4.5	20.7**

Scores are mean ranks for the three performance variables ($df=1$). Sample size is the number of dance episodes.

* $P < 0.05$; ** $P < 0.005$.

at any other perch-zone (Kruskal-Wallis test with multiple comparisons, $P < 0.05$, Hollander & Wolfe 1973). This result suggests that no trade-off occurred between the components of male display. Instead, levels of performance for calling were positively correlated with dancing levels.

Effect of toledo quality

A natural experiment in 1986 suggested that both visitation levels and copulatory success depend upon toledo quality as well as number. Between the 1985 and 1986 seasons the beta male at Perch-zone Z disappeared. The gamma, who became the new beta, apparently had a damaged syrinx. His toledo calling contributed little to the overall volume and resonance of the partnership's toledo output. The quality of the team's dance display did not appear to be affected, except that the beta male's vocalization, given during dance hops, was noticeably fainter than the alpha male's.

The alpha male's effort remained the same, regardless of the quality of his partner's contribution. Female visitation to the zone was reduced both absolutely and relative to other zones. Copulatory success per female visiting was lower in 1986 (17%) than in 1985 (41%) or 1984 (35%). At least one female that visited in 1986 had visited and copulated at Perch-zone Z in 1985. In 1987 Z received neither female visits nor copulations during limited sampling ($N=6$ 2-h observations). A banded, tawny-crowned female, with a history of visits to Z from 1984 to 1986, was seen to visit Perch-zone Y, which had both high quality and output of toledos. Since call output at Perch-zone Z was comparable to that in previous years ($\bar{X}=663.2$), no support exists for a hypothesis of reduced effort due to senescence of the alpha male. Different combinations of males within teams or from different teams differ in toledo quality, which appears to be a function of frequency matching by the partners (J. Trainer, oral communication). Such differences, however, were usually not easily perceptible to human observers.

Residual success of betas and de novo zones

The three turnovers of alpha status all involved replacement, by the previous beta male, of an alpha male that disappeared. In one case (Perch-zone A in June and July 1984) the new alpha male appeared to enjoy residual success (a copulation) despite low levels of toledo output ($\bar{X} \pm SD = 171.8 \pm 147.1$, $N=13$ 2-h observations). A banded female known to have visited under the previous alpha male visited Perch-zone A in 1985. Although the six major perch-zones showed considerable stability in male constituencies from year to year, unpartnered males did do transitory or sporadic displays in other areas. In one case, a

Table VI. Duration of butterfly display relative to that of the preceding butterfly display, in dances culminating with a copulation

	Comparison				Total
	Second versus first	Third versus second	Fourth versus third	Fifth or later versus preceding	
Number that were:					
Longer	19	6	3	2	30
Shorter	15	6	5	2	28
Equal duration	0	1	0	0	1
Mean difference (s)	+1.68	+2.46	-4.88	-0.33	

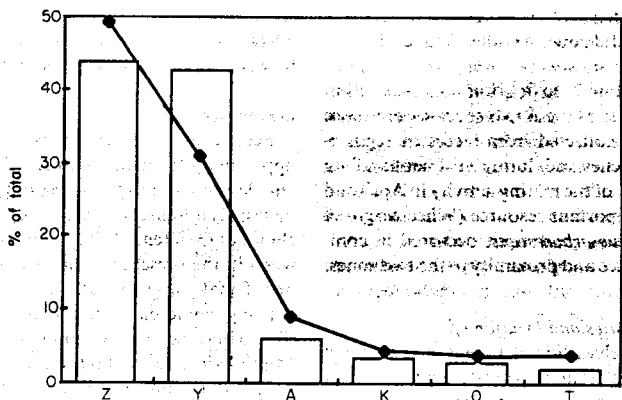


Figure 5. Percentage of total number of hops (line) and total time spent in butterfly display (bars) by males at six major perch-zones in 1985.

partnership may have become established, *de novo*, without assumption of the alpha role by a beta male (Perch-zone C). Unfortunately, the alpha male was the only unbanded partner at any of the zones receiving female visits, so his previous status was uncertain. During the latter part of the 1985 season and during the 1986 season these males called at rates comparable to those of the six major zones ($\bar{X} \pm \text{SD} = 304.4 \pm 248.6$; $N = 28$ 2-h observations) and succeeded in attracting three female visitors, one of whom copulated. The beta partner was 8 years of age in 1986, with previous affiliations at two of the other major perch-zones. Other cases of short-term toledo and dance display by affiliates of major perch-zones occurred sporadically in novel locations but were of short duration (less than 3 weeks). Except at Perch-zone C, the males had ceased, or nearly ceased, display within a week or two of my noticing activity.

Other Possible Factors Affecting Male Mating Success

Morphological traits

Another possible cue for female choice is a morphological trait. An obvious candidate would be tail length, which affects male success in the widowbird, *Euplectes progne* (Andersson 1982). I found no relationship between tail length and success. Indeed, the highly successful alpha at Zone A in 1983 and 1984 ranked 36th out of 37 adult males in tail length and his tail was noticeably shorter than that of his beta partner (10 cm beyond

tail versus 12.4 cm). Conversely, the male with the longest tail yet measured (an alpha male of unknown age) has not yet been notably successful in attracting visits and did not succeed in copulating during my observations. In contrast, a pronounced negative correlation exists between weights and the age and status of males in long-tailed manakins (McDonald, in press). This negative correlation, however, is likely to be a cost of male exertion in performance rather than a basis for female choice. Weights of males in definitive plumage during the breeding season (greater than 3 years of age; $\bar{X} \pm \text{SD} = 17.61 \text{ g} \pm 0.82$; $N = 42$) differed significantly both from weights of females ($\bar{X} = 20.56 \pm 1.89$; $N = 82$) and from weights of definitive males in the non-breeding season ($\bar{X} = 19.87 \pm 0.27$; $N = 8$; $P < 0.01$, GT-2 method, Sokal & Rohlf 1981).

Location of food resources

Location of fruit resources could affect male success either by minimizing foraging time and maximizing energy intake or by attracting females to the general area. A preliminary survey of the 1-ha gridded plots surrounding the primary dance-perch in the most successful perch-zone (Z) and a less successful perch-zone (Perch-zone O) showed that the density of *Hampea appendiculata* (greater than 8 cm diameter) was greater at O (48/ha) than at Z (17/ha, $\chi^2 = 14.8$, $df = 1$, $P < 0.001$). The 17 trees at Perch-zone Z may have been a more than sufficient resource, but it is clear that Perch-zone O

was at least not deficient in this resource relative to the more successful zone. Another frequently used fruit, *Citharexylum donnell-smithii*, was present at pasture edges within 75 m of O but none was within 150 m of Z. Seeds of these two species were those most frequently collected from faeces or regurgitation under perches and during mist net handling during the height of the mating activity in April and May. A third important resource (Wheelwright et al. 1984), *Acnistus arborescens*, occurred in comparable abundance and proximity to the two zones.

Limited display sites and location effects

Perches themselves did not appear to be a limited resource. At least four previously active primary dance-perches became overgrown or were destroyed by treefalls during this study. In each case, the males immediately transferred to a previously unused or little-used perch in the immediate vicinity, without apparent reduction in success. Success shifted within the study area in concert with performance but without apparent relationship to resources or to the physical configuration of the habitat (e.g. habitat bottlenecks that would tend to concentrate females moving through the area). The physical configuration did not change (e.g. by pasture clearing) during this study, nor during at least the preceding 30 years (A. Hoge, unpublished data).

Male-male interactions

Male-male interactions are important in establishing male ranks within zones. Only the top males in a team, usually the alpha and beta male, had access to females during dance displays. The alpha and beta roles appear to determine which male within a partnership will remain for the solo display that precedes copulation. Of 117 copulations observed, alpha males performed all but two. For the exceptions, the alpha male was temporarily absent from the area of the dance-perch. In all cases where a dual-male display continued to the point where one male left and the other began solo butterfly display, it was the alpha who remained ($N = 153$, seven different alphas). Thus, females do not appear to have the option of choosing within a partnership. Although alphas chase away any male that appears in the vicinity of the perch during solo display, I have no evidence for disruptions of a male's copulations by other males. While male-male interactions (intrasexual selection) may be

crucial to a male's success they do not appear to affect the opportunity for females to choose between teams displaying at different perch-zones.

Female-female interactions

Female-female interactions might decrease the opportunity for female choice in three ways: (1) if females were to restrict access of females to certain males; (2) if females were to copy another female's choice or (3) if females were more likely to copulate when in the presence of other females. Since only one female ever copulated per dance display, copying would entail return of a 'watcher' female that witnessed a copulation by another female. Multiple-female facilitation, on the other hand, would result immediately in a higher probability of copulation by at least one female. In 1984 and 1985, 214 dances were for a single female, 54 dances were for two females, three for three and two for four females. An agonistic interaction (brief chase) between females occurred only once.

A banded female that watched another female copulate was seen to return to the same zone for a later copulation. Two other banded females returned for copulations after watching dances for another female that did not copulate. The proportion of single-female dances that were successful was 0.27. If more than one female watches a dance, and assuming independence, the probability that none will copulate is $(1 - 0.27)^n$, where n is the number of females. With two females the expected frequency of 'failure' is 0.46. With three females the expected frequency is 0.40 and for four females, 0.29. This generated an expected 32.4 'independent' copulations; the observed number was 32. Thus, I conclude that dances for multiple females were not more likely to lead to copulations than were dances for lone females.

DISCUSSION

The data from this study are consistent with the hypothesis that male performance of courtship displays is a basis for female choice. Females have home ranges of as much as 80 ha that would allow sampling of 55 or more males per season, including six to eight well-established zones with consistent levels of display. Such sampling would not require appearance within the immediate area of the perch, because the toledo call carries 50–200 m, depending upon wind conditions. Although females may have

little opportunity for mate choice within a zone, they appear to have the opportunity to choose between five to eight major perch-zones. The alpha male at each zone, in turn, stands at the apex of an extensive system of male-male interactions (McDonald, in press).

Correlates of Male Mating Success

Male performance of courtship display correlated with male copulatory success and differed between male teams. That such correlates exist indicates that, if females are choosing, they are using the same sets of cues. The performance correlates fit a model of hierarchical mate choice. Having used the toledo call as a wide ranging cue for deciding which perch-zones to visit, females may use dance display as a criterion for copulatory receptivity at the very few zones where they actually watch dance displays. Other males were often seen on or near the dance-perch during toledo bouts and were tolerated at all times except in the immediate vicinity of the dance-perch during the relatively brief female visits. Thus the toledo call seems to function purely to attract females and not to repel other males.

A caveat in considering such correlative data is Gibson & Bradbury's (1985) suggestions that the critical cue may not have been quantified but was simply correlated with the measure of performance tested. This may be particularly applicable to the butterfly display correlate, because of the multiplicity of visual and auditory stimuli available as potential cues. The toledo call, on the other hand, is most likely to be monitored at a distance, without recourse to visual or other auditory stimuli. A further caveat is that correlation might involve reverse causation. That is, male performance might be a response to female behaviour rather than vice versa. Female behaviour during courtship display undoubtedly influences that of males. The data on duration of butterfly displays that preceded copulations (Table VI), however, provide evidence against such reverse causation, for at least one behaviour correlated with mating success.

Male Traits Selected

High levels of toledo calling require the almost constant presence of the male partners, reducing the amount of time available for maintenance behaviours. Butterfly flight appears laboured, inefficient and energetically expensive. Data on weight

loss as a function of increasing age and status of males and of breeding versus non-breeding season suggest that display may be a considerable energetic drain. It is interesting, therefore, that performance levels were positively correlated within zones, such that the top teams at Perch-zones Y and Z performed at the highest level for every measured performance variable that correlated with success in visitation and copulation.

An alternative hypothesis is that weight loss might be an adaptive response to a requirement for manoeuvrability during the dance displays (Lill 1976). Butterfly flight may have a further cost in 'riskiness' for the alpha male. On seven occasions, at three different perches, the beta male attempted a copulation during the dual-male phase of butterfly display. In five cases, the female appeared to be receptive, but the alpha male chased the beta male away, probably before any transmission of sperm. An alpha male, therefore, may have to weigh the increasing probability of female receptivity against increasing risk that a proportion of the paternity will accrue to his partner rather than himself. Under an 'honest advertising' system (Kodric-Brown & Brown 1984) a male could signal the extent of his dominance by undertaking a risky behaviour. The riskiness of butterfly flight might help explain why it, rather than number of hops, is correlated with success. Under the 'runaway' model of sexual selection (Lande 1981) the particular traits that are selected and become exaggerated would represent non-adaptive evolution of traits that covary with the characters controlling choice in females.

The phenotypic correlates that may be subject to female choice involve only the top displaying males. It should be noted, however, that a male's being able to display as a member of a team with top levels of performance is conditional upon a number of factors. First, he must survive for 8 or more years. Second, he must establish a ranking within a perch-zone. Third, he must form an alliance that can generate a considerable quantity of joint display, perhaps involving extensive practice. This preparatory stage depends almost exclusively upon male-male interactions (McDonald, in press). Male mating success, therefore, is conditional upon long survival, male-male interactions (intrasexual selection with cooperation) and upon cooperative male performance subject to female choice (intersexual selection). The strict alpha precedence at each perch-zone and the lack of

disruptions contrasts with the importance of disruptions in the congeneric swallow-tailed manakin *Chiroxiphia caudata* (Foster 1983) and the Guianan cock-of-the-rock (Trail 1985a). In general, younger birds tend to reproduce less well (Curio 1983). If females choosing less successful zones are indeed 'naive' and younger, then males at the most successful zones may be even more successful than the number of mates would suggest. In the method of Wade & Arnold (1980) for partitioning reproductive success, males with the highest component of total opportunity for selection due to sexual selection (I_s) would gain increments to total reproductive success (I_m) via the success of their mates (I_p).

Alternative Determinants of Male Success

Morphological traits

The data did not support the hypothesis that mate choice was based upon the most obvious morphological cue, tail length. This trait has served as the paradigm of a sexually selected trait (e.g. Arnold 1983). A more critical test of the importance of morphological traits will require a larger sample of measurements in alpha males, holding age, or at least duration of alpha status, constant. Morphological characters such as tail length or plumage brightness may prove to be threshold traits, such that females require only a baseline level of trait development. Although brightness of male definitive plumage appears to be uniform, quantitative comparisons of alpha male plumages would be instructive.

Mate choice copying

The data concerning copying are insufficient for a conclusive resolution of the question. The fact that the expected and observed totals for multiple female visits did not differ suggests that females were not more likely to copulate in the presence of other females. Given that male-male interactions produce a small subset of alphas that are 'eligible', and that significant differences in display performance exist even between alphas (or more strictly their partnerships), it is probably not necessary to invoke copying in order to explain high variance in male copulatory success. Long-tailed manakins may, however, meet the conditions for copying in a model by Losey et al. (1986) in which copying is likely to evolve if (1) some females are capable of

acute discrimination, (2) fecundity is low, and (3) prolonged assessment and multiple visits are possible.

Location effects

Male performance of courtship display seems to define the mating centres. This result echoes both recent re-evaluation of mating success within clusters of sage grouse, *Centrocercus urophasianus* (Gibson & Bradbury 1985). As for Guianan cock-of-the-rock, *Rupicola rupicola* (Trail 1985b), male-male interactions before female arrival were important in mating success. Unlike that system, however, disruptions and territorial intrusions did not impede near unanimity of female choice based upon display. Although no correlation was apparent between fruit resource location and male display levels careful, intensive and extensive mapping of resources relative to male location would be necessary to test adequately the hypothesis that proximity to a wider spectrum of resources promotes vigour of male display.

'Hotspot' model

Bradbury et al. (1986) have modelled hotspots for male settlement. A hotspot is an area with high overlap of female use of space. Perch-zones of long-tailed manakins appear to be rather uniformly spaced. If each perch-zone is considered an arena with two displaying males, long-tailed manakins have an 'exploded' lek pattern. If, however, each perch-zone is considered to include the 3-15 male affiliates ($\bar{X} \pm \text{SD} = 7.1 \pm 3.4$, $N = 21$ perch-zones) that I noted, then the number of males per lek is closer to that of other lek species and other manakins (Lill 1974). The model of Bradbury et al. (1986) predicts uniform spacing with extremely large female home ranges. If food resources tend to be unpredictable in space and time, and given the very large home ranges of female long-tailed manakins, no location may qualify as a hotspot. Building a reputation as a top performing team probably requires remaining in the same, predictable location. Tentative evidence for de novo establishment of perch-zones suggest that this may be a rarely used alternative, rather than a short-cut to success, since the alpha male was probably no younger than many of those that assumed the alpha role from their role as beta males. Periodic establishment of de novo zones may represent a balance between the probability of moving to alpha status at an established zone and the probability of

establishing an effective partnership at a novel location. The location of male clusters might, however, be arbitrary with respect to the distribution of resources or the distribution of non-mate choice activities of females. Comparative studies of male location and female use of space in other species of manakins would serve both as tests of the hotspot model and to elucidate the nature of the interaction between resource distribution and the mating system.

Correlates of male mating success suggest that females may be discriminating rather finely between six to eight alpha males and their partners, in a group of approximately 55 displaying males per season. The lack of opportunity to choose within zones may actually facilitate unimpeded female choice between zones by preventing disruptions. That significant differences in performance exist between the few top teams, indicates that considerable phenotypic, if not also genetic, variance exists even within the small subset of males that have reached a stage where they are eligible for female choice. If female acuity of discrimination and high variance in mating success preceded the evolution of cooperative display, the variance itself may have acted as a constraint favouring cooperation. Cooperation may enhance future prospects for reproductive success of younger males. Females, with lifelong reproductive spans, may overlap several successive alphas, thus providing a direct, if delayed benefit to a young male's present efforts in courtship display (McDonald, in press). Alternatively, dual-male display might exaggerate apparent differences between males and increase the ease with which females discriminate between partnerships. This hypothesis, however, requires an unspecified constraint favouring prior evolution of cooperation and thus appears less parsimonious. A comparative approach may be the most useful in determining the probable sequence of evolutionary steps.

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