

LIGHT PATTERNS AS CUES FOR MATE CHOICE IN THE LEKKING WHITE-THROATED MANAKIN (*CORAPIPO GUTTURALIS*)

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ABSTRACT.—We explored in an exploded lek species the relationships between three alternatives hypotheses for typical skewed male mating success: (1) female preference for display-site characteristics; (2) female preference for male phenotypic traits; and (3) mate choice determined by the outcome of male dominance interactions. The possible role of these mechanisms of female choice was examined in the White-throated Manakin (*Corapipo gutturalis*), a species in which males display on the top of mossy fallen logs lying on the primary forest floor. Data on light intensity at the display site, lek attendance, male calling and display rates, visits by males and females, and mating success were collected on six males at a single lek. The two males with the brightest two arenas received high rates of female visitation and performed 71% of the mating attempts. However, only one of them successfully copulated because the other male was always disrupted by visiting males. The results suggest that light properties of the display site and attendance of the male determine the attractiveness of male display to females, whereas male interactions subsequently mediate copulatory success. Brightness of the display site appears as the primary cue for mate choice in *C. gutturalis*, but this is not used by females as an indicator of the males' relative dominance because the dominance status of males is not correlated with the brightness of their display sites. Received 23 April 1993, accepted 19 August 1993.

IN LEK MATING SYSTEMS, males aggregate and display to attract females rather than defend females directly or monopolize resources females need. Females visit males only for mating and appear fairly free to choose among potential mates (Bradbury 1981, Bradbury and Gibson 1983). The high mating skew typical of lek species (Bradbury and Gibson 1983, Bradbury et al. 1985) argues for strong and convergent choice by females for certain male or site characteristics. Three alternative hypotheses have been suggested to explain these female preferences: male phenotype, display-site characteristics, and female copying (reviews in Bradbury and Gibson 1983, Balmford 1991). These hypotheses have been tested only at "classical leks" (Bradbury 1977, 1981) or "true leks" (Oring 1982), where males are densely clustered within sight of each other. In this paper, we explore the relationships of territory characteristics, male behavioral characteristics, and female visit rates at an "exploded lek" (Snow 1970, Bradbury 1981, Foster 1983). This pattern of males spacing, also called "quasi-lek" (Oring 1982) or "court" system (Beehler and Foster 1988), shows loosely clumped display sites that are not within sight

of each other. To explain female preference in dispersed courts species, Borgia (1979) proposed the dominance-indicator model, which combines either female site preferences and/or phenotypic-trait preferences with male dominance.

In the Neotropical manakins (Pipridae), lek mating is the rule and species show a large range of clustering from classical leks to exploded leks. As predicted by the hotspot model of lek evolution (Bradbury et al. 1986), variation in male clustering is correlated with female home-range size among sympatric manakin species, but habitat preferences or attractiveness of certain males may be invoked to explain specific lek siting (Théry 1992). Despite intensive research conducted by Lill (1974a, b, 1976) in Trinidad, no behavioral or morphological cues for female choice are known for any of six sympatric lekking manakins of French Guiana. In the White-bearded Manakin (*Manacus manacus*), experimental studies in which top-ranking males were removed showed no shift in the spatial distribution of female visits and mating, suggesting female preference for display location (Lill 1974a). In *M. manacus* and the Golden-headed Manakin (*Pipra erythrocephala*), Lill (1974a, b,

1976) found that, if males compete for the sites preferred by females and only dominant males can gain access to the preferred sites, females would indirectly obtain mates of high dominance status. The only cues for female choice known for manakins are number of unison calls and duration of dual-male display in the Long-tailed Manakin (*Chiroxiphia linearis*; McDonald 1989a). In this species, male mating success is determined by female choice between leks, and by age-based male dominance within leks (McDonald 1989b).

Our study examines the correlates of mating success in the White-throated Manakin (*Corapipo gutturalis*), an exploded lek species inhabiting dense tropical forest in French Guiana (Théry 1990a, 1992). Leks range in size from five to eight males and the nearest-neighbor distance averages $26.2 \pm \text{SD of } 1.7$ m. Each male defends his own display arena centered on a mossy fallen log where all courtship display occurs. Males use a variation of the same display in both female courtship and aggressive threats against intruding males. Display-site characteristics are likely to be important in this species because the location of arenas, the courtship postures, and the nature and disposition of color signals on males have been shown to be related to specific light patterns falling on the display logs (Théry 1987, 1990b). Since females only visit arenas singly, copying is unlikely to affect mate choice in this species. Data were collected on light parameters, display behavior, female visits, male interactions, and mating success to examine the possible role of site differences, male attributes, and male dominance as cues for female mate choice.

METHODS

This study was conducted in French Guiana at the Nouragues biological station (4°03'N, 52°42'W; undisturbed primary tropical rain forest; site described in Erard et al. 1989, Julliot and Sabatier 1993) from 10 October to 15 December 1990 (dry season). All measures and observations were made at one *Corapipo gutturalis* lek, comprising six mossy fallen logs. Locations and number of display sites were unchanged since their discovery in 1987.

Measurements of light intensity (irradiance in W/m^2) were made with four analogic pyranometers possessing cosine heads sensitive from 400 to 700 nm (Ecosolaire, Paris). Outputs were directly proportional to the assumed response of visual receptors (Lythgoe 1979). For each pyranometer, data were collected

800 times per minute through the expansion port of a Canon X-07 microcomputer and recorded on a Canon X-730 cassette recorder. The water-resistant system was powered by two 12-V batteries and calibrated between each site. Sensors were placed against one side of the log, levelled with the upper surface and vertically fitted using a plumbline. Along each log, one sensor was placed at the center of the display zone, two were placed 2 m each side of the display zone, and one was placed at 4 m from the display zone. Measurements were taken continuously from dawn to dusk. Brightness contrast, computed as the light intensity measured at the central display zone divided by mean light intensity measured at 2 and 4 m, is an important component of a manakin's light environment (Théry 1987, 1990b) and was used to evaluate visibility of adult male displays against the background. In order to compare light environments independently of the weather, 18 sunny days showing more than 90% cloudless sky were selected for light monitoring. During the three days of study at each site, we averaged every 6 min the 4,800 light-intensity values measured by each sensor. For each display site, daily mean light intensity was computed as the average of these 360 6-min mean values. The same procedure was used to compute daily mean values of brightness contrast.

At each site, behavioral observations were synchronized with standard time and conducted on separate days from the light monitoring because the solarimeter device could have influenced male display behavior and female visits. To minimize disturbance, only one adult male and one female were banded at this lek before the study period. Previous studies conducted at other leks (Théry 1990a, b, 1992) and individual banding of males in October 1992 and September 1993 showed that each log owner displayed on the same mossy log for at least one breeding season and visited neighbors within the whole cluster. Four immature males were individually recognizable from unique patterns of transitional plumage. All log owners were fully adult males. Each arena was observed for a total of 100 h equally distributed throughout the day. The following behaviors were recorded: number of advertisement calls per hour of observation; number of wing-snap displays per hour of observation; number of male and female visits; social interactions between resident males and visitors, such as disruptions; copulation attempts; successful copulations; location and duration of sun patches; and percentage of time the resident male was in attendance. Disruption, which involved young as well as adult males, always refers to mating interruption since female visits were never disrupted prior to attempted mating. Several additional variables were derived from these observations, including advertisement call rate per minute of attendance, disruptions per visiting female, and disruptions per visiting male.

To avoid pseudoreplication, mean values of these

behavioral, social, and site variables were computed for each arena. Thus, despite the large sampling effort, the sample size for many of the comparisons was only six. The errors of these estimates are believed to be low, however, because of the long sampling times. All variables except wing-snap displays were slightly skewed and, therefore, were log-transformed to meet the normality requirement for parametric statistical tests. Only copulations could not be satisfactorily transformed. We used Pearson correlation coefficients to examine the simple correlations among these variables, and partial correlation and path analysis to determine which correlations were meaningful and which were spurious.

Path analysis (Wright 1934, Li 1986) is a tool for investigating the possible cause-and-effect relationships in a correlational dataset. The objective is to find the best model of causal interrelationships among the variables that predicts the observed simple correlation matrix. A proposed model specifies which links between variables are due to direct causation, which are indirect via an intervening variable, and which are spurious. Direct effects are indicated by a single-sided straight arrow, and all unresolved or unanalyzed correlations are indicated by a double-headed curved arrow. A path coefficient is computed for each direct effect that indicates the independent strength and direction of the relationship between the two variables, controlling for any other direct effects on the dependent variable. The path coefficients are standardized beta coefficients from a multiple-regression analysis of each dependent variable in the model and all direct effects acting on that variable as proposed by the model. The predicted correlation coefficient of any pair of variables in the model is then computed by multiplying the coefficients in each causal path linking the two variables and adding these products over all valid connecting paths. An estimate of the overall fit of the model is determined by taking the sum of the squared differences between all pairs of observed and predicted correlation coefficients, and subtracting this value from 1 (i.e. $r^2 = 1 - \Sigma[r_{\text{pred}} - r_{\text{obs}}]^2$). The relative predictive power of two or more alternative models can thus be compared quantitatively, although such comparisons should involve only pairs of variables that are shared between the two models (see Wootton 1994). With more substantial datasets than ours, the program called LISREL can be used to aid the search for all alternative models and determine a statistical fit to the data using maximum-likelihood estimation. In all types of structural modelling, the user must specify the known causal relationships to constrain the number of possible arrangements. The simpler path-analysis technique, which we use here, involved only manipulations of the correlation coefficients, so the sample size upon which the correlations are based does not enter in the computation. However, the exercise is only as good as one's confidence in the correlation coeffi-

TABLE 1. Light intensity and brightness contrast (daily average \pm SD, $n = 120$) at six arenas.

Arena	Light intensity (W/m^2)	Brightness contrast
1	46.38 \pm 115.55	5.02 \pm 9.14
2	8.49 \pm 18.21	0.98 \pm 1.55
3	15.51 \pm 18.56	1.89 \pm 1.41
4	12.33 \pm 23.57	0.80 \pm 0.66
5	10.20 \pm 7.26	1.86 \pm 1.64
6	42.45 \pm 122.98	2.58 \pm 7.53

cients, and no statistical test of the significance of a given path model is possible. Because of this lack of statistical proof, we use the technique to identify the best-fitting model, recognizing that experimental manipulations and data from other leks will be required to corroborate the model.

RESULTS

Light intensity and brightness contrast at display sites.—Daily patterns of light intensity were consistent at each site. Light-intensity peaks appeared at the same time on sunny days, and correlations always were positive and significant between measurements taken at one site on different days ($n = 120$, all $P < 0.01$). The 6-min mean values taken at the same time of the day, therefore, were averaged across the three sunny days of recording at a site, and were used to compare light characteristics of display sites. Arenas were characterized by one of three different light patterns (Table 1):

(1) High intensity and high contrast. Arena 1 was brightly illuminated by four temporal sun patches of increasing intensity, lasting 10 to 40 min (Fig. 1), which gave this arena a high daily mean intensity. Light intensity at 2 and 4 m was very low during these periods, leading to 6-min mean values of brightness contrast higher than 20 (Fig. 2). Arena 6 also showed high daily mean light intensity, but from only two sun patches. Daily mean brightness contrast was lower at Arena 6 (Table 1), although 6-min mean values were similar for the peaks (Fig. 2). Correlations between daily distributions of light intensity and brightness contrast were positive and highly significant at both display sites ($r > 0.95$, $n = 120$, $P < 0.001$).

(2) Low intensity and low contrast. Although Arenas 3 and 5 showed lower daily mean light-intensity values than Arenas 1 and 6, display sites were still more intensely illuminated than

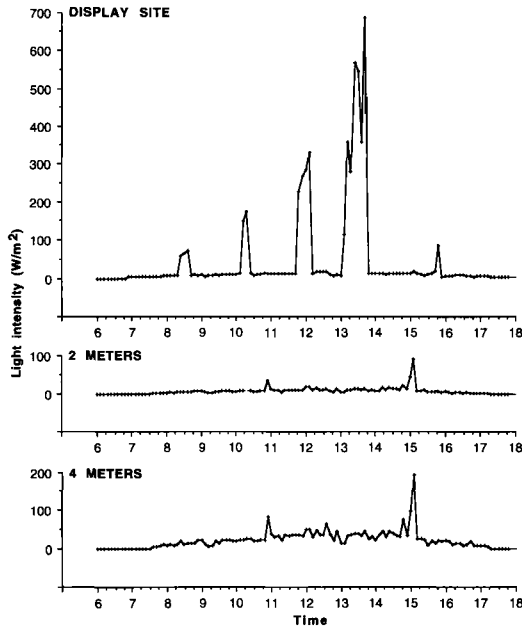


Fig. 1. Daily pattern (from 0600–1800) of 6-min mean values of light intensity at Arena 1.

other parts of the logs (Fig. 3). At both arenas, daily mean brightness contrast averaged 1.9 (Table 1) and short-term peaks reached 6.0 (Fig. 2). Light intensity was correlated with brightness contrast at Arena 3 ($r = 0.51$, $n = 120$, $P < 0.001$). Arena 5 showed higher peaks of light intensity in the surrounding than at the display site, and brightness contrast was independent of light intensity ($r = -0.04$, $n = 120$, $P > 0.05$).

(3) Low intensity and reversed contrast. Although Arenas 2 and 4 were illuminated briefly by sun patches, light was more intense in the surrounding areas (Fig. 4), leading to daily mean values of brightness contrast lower than 1 (Table 1). However, correlations between light intensity and brightness contrast were significant at Arena 4 ($r = 0.29$, $n = 120$, $P < 0.01$), but not at Arena 2 ($r = 0.09$, $n = 120$, $P > 0.05$).

Brightness contrast was significantly correlated with light intensity for the lek as a whole ($r = 0.82$, $n = 6$, $P < 0.05$). In all stepwise regressions of behavioral variables with light intensity and brightness contrast as independent variables, each one eliminated the other. This means that light intensity and brightness contrast were measuring the underlying variable, so we combined the two into one variable called "light" by standardizing their log values and adding the standard scores together.

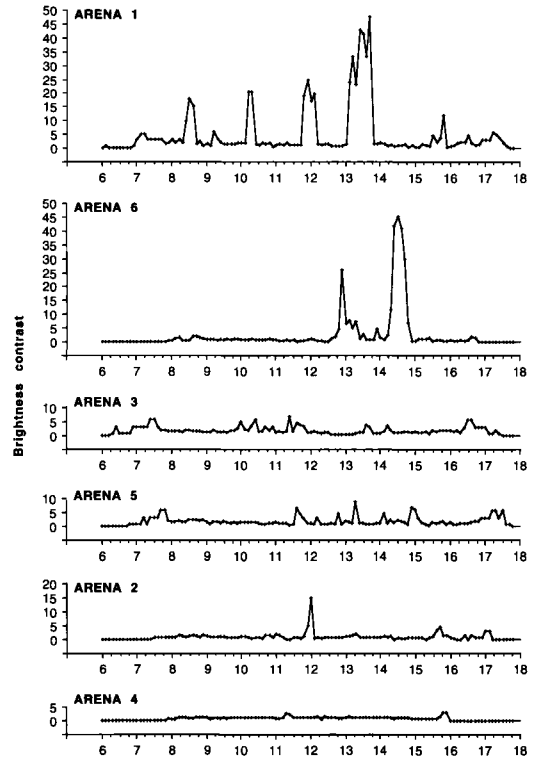


Fig. 2. Daily pattern (from 0600–1800) of 6-min mean values of brightness contrast at six arenas.

Distribution of female visits, male visits, and mating.—During the entire 600 h of sampling, there were 131 female visits, 72 male visits, 41 attempted copulations, and 9 successful copulations. Distributions of these events among the six males are shown in Table 2. Males received unequal numbers of female visits (Table 2, $X^2 = 33.93$, $df = 5$, $P < 0.001$). Males 1 and 6 were visited frequently, whereas the other males rarely were visited by females. Male 1 attempted 14 matings, and 9 resulted in successful copulation. All copulations were observed between 1300 and 1400 on the same 40-cm-long section of log (Fig. 5). Male 6 attempted 16 matings, but was always disrupted by other adult males. Males 2, 3, 4, and 5 rarely attempted to mate, and were always disrupted. Mating females stayed more briefly on the log ($\bar{x} = 29.9 \pm SD$ of 2.8 s, $n = 9$) than when leaving without copulating (56.6 ± 26.9 s, $n = 122$; Mann-Whitney U -test, $P < 0.01$). Male visits were frequent, but they did not always result in mating disruption. Fifty-four of the 72 male visits occurred during female visits, and 32 of these (59.3%) lead to

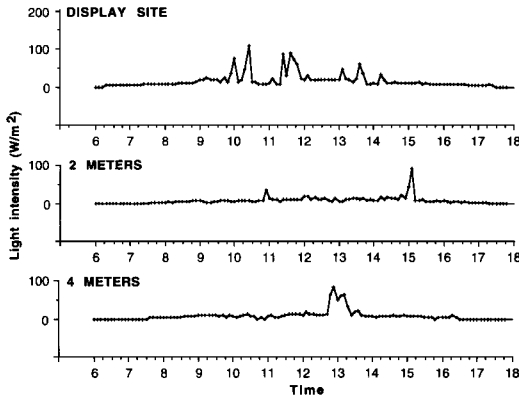


Fig. 3. Daily pattern (from 0600-1800) of 6-min mean values of light intensity at Arena 3.

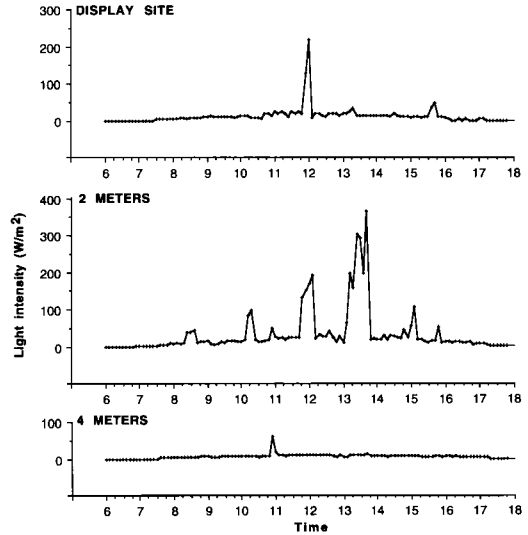


Fig. 4. Daily pattern (from 0600-1800) of 6-min mean values of light intensity at Arena 4.

disruption of mating. On all other occasions, visiting males observed the owner's courtship of the female from perches around the display log. The fraction of male visits that resulted in disruption varied from a low of 25% for Males 1 and 2 to a high of 67% for Male 6. The fraction of female visits that were disrupted showed a similar pattern.

Daily light patterns as correlates of female visits and male mating success.—Parts of mossy logs lit by sun patches and surrounded by darker understory formed the typical light habitat of Males 1 and 6. These males, displaying at arenas with highest values of light intensity and brightness contrast, received significantly greater numbers of female visits, but copulation was only observed at the arena exhibiting the highest brightness contrast. On a daily scale, female visits were correlated with light intensity at Arenas 1, 3, 4, and 5, and correlated with brightness contrast only at Arena 1 (Table 2). Therefore, Arena 1 was the only display location showing high values of light intensity and brightness contrast significantly correlated with the daily pattern of female visitation. At this arena, sun patches were present at the time of female visits and the understory was relatively very dark. Copulation only occurred under these contrasted light conditions, with at least 20 times more light at the mating location than in the surrounding area.

Male display behaviors.—The display repertoire of log owners consisted of simple advertisement calls given from 4- to 8-m-high specific perches, perch displays, flight-song displays, butterfly log-approach displays, wing-snap dis-

plays, rebounds from log with turn around in flight, bill-pointing postures, to-and-fro displays, and display postures with foreparts lowered to the log, including wing-shiver displays (Prum 1986, Théry 1990a). The wing-snap display is highly conspicuous and involves a rapid approach to the log from the canopy, synchronized display calls and a mechanical wing noise at the end. The analysis of two 16-mm film sequences taken at 500 frames/s of the wing-snap

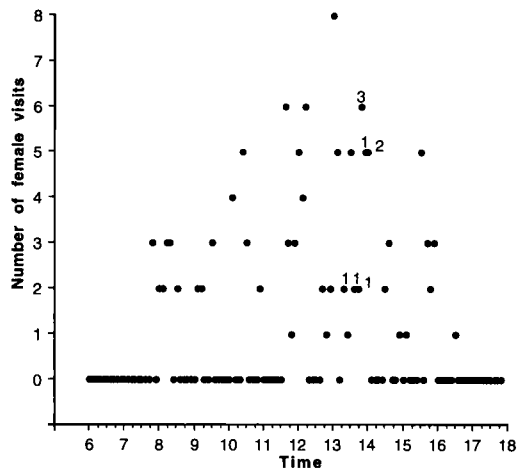


Fig. 5. Daily distribution of female visits at six arenas. Number of copulations for 6-min periods indicated.

TABLE 2. Distribution of lek attendance, calling, wing snapping, female and male visits, disruption and copulation rates among adult males. Percent of total given in parentheses. Pearson correlation coefficients between light variables and female visitation within males.

Statistic	Male					
	1	2	3	4	5	6
Lek attendance (% observation time)	88	72	51	48	45	68
No. advertisement calls per hour observation	193 (43.0)	123 (27.4)	30 (6.7)	28 (6.2)	34 (7.6)	41 (9.1)
No. wing-snaps per hour observation	4.1 (14.7)	5.4 (19.4)	2.7 (9.7)	3.8 (13.7)	5.5 (19.8)	6.3 (22.7)
Number of female visits	42 (32.1)	19 (14.5)	13 (9.9)	11 (8.4)	15 (11.4)	31 (23.7)
Number of male visits	20 (27.8)	12 (16.7)	4 (5.6)	5 (6.9)	7 (9.7)	24 (33.3)
Number of disruptions	5 (15.6)	3 (9.4)	2 (6.2)	3 (9.4)	3 (9.4)	16 (50.0)
Percentage of disruption per female visit	11.9	15.8	15.4	27.3	20.0	51.6
Percentage of disruption per male visit	25.0	25.0	50.0	60.0	42.9	66.7
Number of copulations	9 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Correlation of light intensity vs. female visits*	0.19*	0.07 ^{ns}	0.24**	0.21**	0.25*	0.12 ^{ns}
Correlation of brightness contrast vs. female visits*	0.19*	0.09 ^{ns}	0.04 ^{ns}	0.12 ^{ns}	0.13 ^{ns}	0.10 ^{ns}

*, $P < 0.05$; **, $P < 0.01$; ^{ns}, $P > 0.05$.

* $n = 120$.

display (filmed by A. R. Devez, CNRS URA 1183) showed that adult males reach the understory at a speed of 100 to 120 km/h, then open their wings just above the log, producing the whip-like wing noise and tracing an horizontal S-pattern in the air, and finally drop to the log. This high-speed display is undoubtedly more costly energetically than advertisement calls or log displays. All copulations occurred after a single display with wing snap, preceded by a series of advertisement calls, to-and-fro displays, and wing-shiver displays. On the contrary, a series of wing snaps was always performed by males in aggressive encounters with intruding males at a display site.

Table 2 shows the number of advertisement calls per hour of observation, the number of wing-snap displays per hour of observation, and the percentage of time the male was in attendance at his log site. Males 1 and 2 both exhibited high lek-attendance levels, as well as very high rates of advertisement calling, compared to the other four males. The number of wing-snap displays per hour showed considerably less variation among the males and was not obviously associated with attendance or calling.

Alternative hypotheses for female choice.—Table 3 summarizes the correlations among behavioral, site, and visit variables. Several of these correlations were very strong and significant despite the small sample size. The most significant correlations are plotted in Figure 6 to demonstrate that they are indeed robust and not

due to single point outliers. We used these correlation results, in combination with partial-correlation and path-analysis techniques, to explore the alternative hypotheses for female choice: female preference for site characteristics, such as light intensity and contrast; female preference for behavioral traits, such as call rates, display rates, and attendance; and female preference for traits that indicate a male's dominance status, quality, or vigor.

The number of females a male attracted to his site was significantly correlated with attendance, light, male visits, and mating attempts. These four variables were also intercorrelated. The number of mating attempts was obviously a consequence of female visits. Similarly, the number of male visits was assumed to be a consequence of female visits, since other males primarily visited an arena when a female was present for the explicit purpose of disrupting any copulation attempts by the resident male. Light and attendance were, therefore, the only variables potentially influencing female visits. In partial-correlation analyses of each of these variables with female visits, both had strong independent effects (light vs. females, partial $r = 0.844$, $P = 0.072$; for attendance vs. females, partial $r = 0.878$, $P = 0.050$). No other behavioral variables such as call rate or display rate were significantly correlated with female visits. Call rate per minute on the arena was strongly, but not significantly, correlated with attendance. The observed correlation between call rate and

female visits completely disappeared after partialling out attendance, indicating that this association was indeed spurious. Finally, there was no evidence that any measure of a male's ability to prevent disruptions, measured as percent of visiting females disrupted or percent of visiting males disrupting, determined his ability to attract females to his site. Since the visit rate of females may not be an accurate indicator of a male's attractiveness to females as mates, we repeated all of these correlation analyses with number of copulation attempts, which is the same as female solicitations. The results parallel those for female visits. Light was somewhat more strongly correlated with copulation attempts than attendance. Call rate, display rate, and disruptions per female and per male were statistically nonsignificant as before. Male visits and number of disruptions were highly correlated with copulation attempts and deemed to be consequences of female solicitation.

No variable by itself was significantly correlated with the number of copulations using either Pearson or Spearman rank correlation. Behavioral observations clearly indicated that, in order to copulate successfully, a male not only had to attract females to his site, but he also had to prevent visiting males from disrupting the copulation attempt. All males were solicited by females, but only Male 1 successfully copulated. Therefore, the number of visiting females should have shown a strong positive correlation with copulations, and disruptions should have shown a strong negative correlation. These effects were obscured because both female visits and disruptions were strongly and significantly correlated with male visits. In a multiple-regression analysis of the dependent variable copulations, considering female visits and disruptions as independent variables, the expected strong positive effect of female visits and strong negative effect of disruptions became apparent. We are not justified in testing the significance of these partial relationships because of the non-normal distribution of copulations. No other variables showed any type of strong association with copulations after controlling for female visits and disruptions.

We used path analysis to construct a causal model reflecting the simple- and partial-correlation analyses. Many alternative arrangements were examined to arrive at the best-fitting model shown in Figure 7. We proceeded as follows. The multiple regression of female visits and

TABLE 3. Pearson correlation coefficients among all behavioral and light variables ($n = 6$ for all comparisons). All variables log-transformed except displays and copulations.

	Attendance	Calls	Call rate	Displays	Female visits	Male visits	Disruptions per male	Disruptions per female	Light	Copulations attempts
Calls	0.896*									
Call rate	0.789	0.980***								
Displays	0.223	0.142	0.096							
Female visits	0.886*	0.730	0.611	0.397						
Male visits	0.830*	0.646	0.521	0.667	0.931**					
Disruptions	0.476	0.131	-0.033	0.676	0.699	0.832*				
Disruptions per male	-0.522	-0.834*	-0.918**	0.064	-0.325	-0.198	0.377			
Disruptions per female	-0.215	-0.544	-0.654	0.551	-0.016	0.238	0.703	0.851*		
Light	0.617	0.398	0.273	0.079	0.855*	0.669	0.621	-0.041	0.018	
Copulation attempts	0.718	0.458	0.311	0.462	0.913**	0.908**	0.886*	0.047	0.331	0.847*
Copulations	0.699	0.749	0.722	-0.197	0.725	0.484	0.143	-0.559	-0.522	0.722
										0.586

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

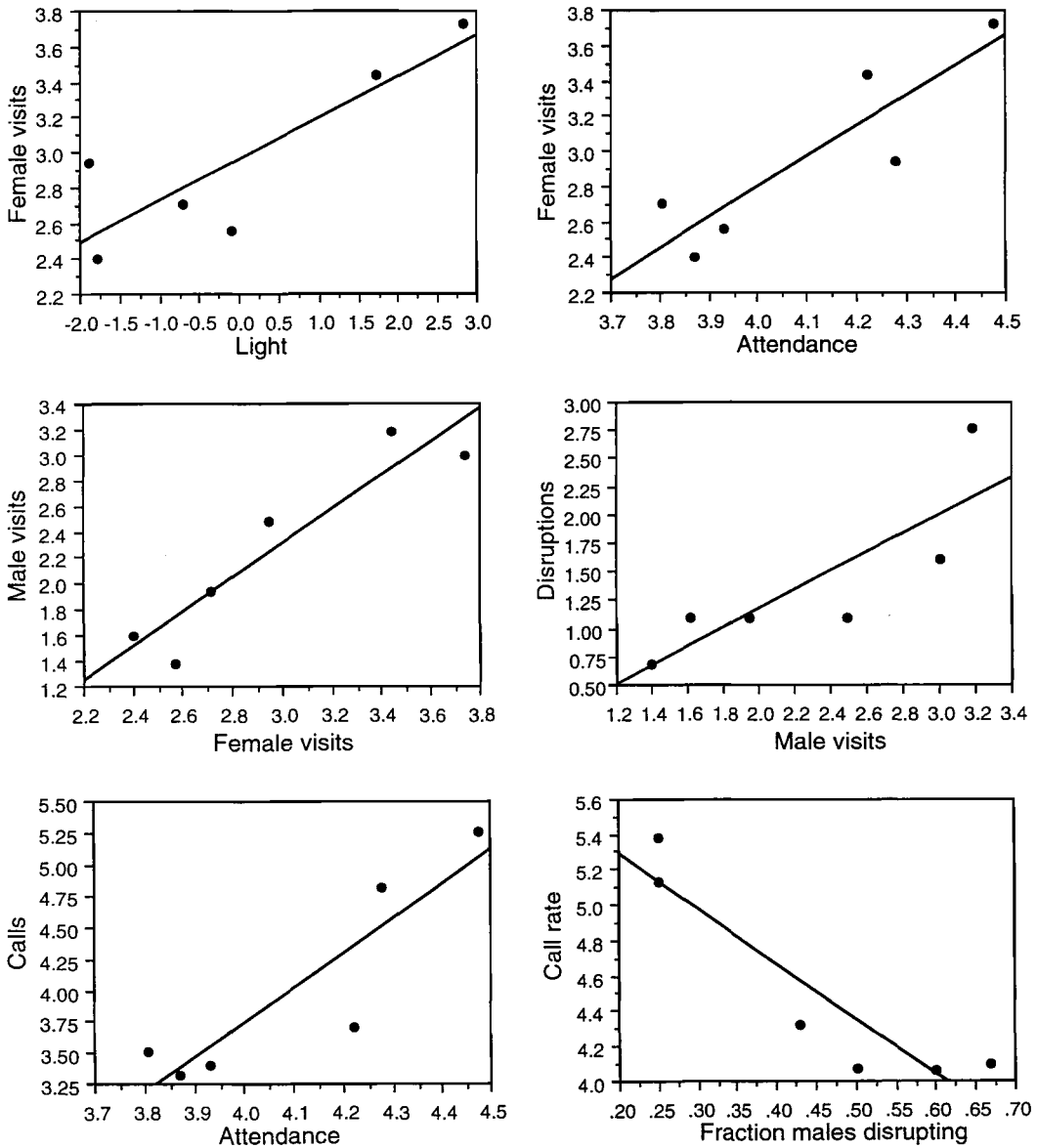


Fig. 6. Plots of most significant correlations computed of site characteristics, male behavioral characteristics, and visits rates. All variables log-transformed, except the fraction of visiting males disrupting copulation attempts.

disruptions on copulations produced the path coefficients relating these two direct effects (1.224 and -0.713 , respectively). The path coefficient for the direct female effect was greater than one because of the strong confounding effect of male visits on female visits and disruptions. These coefficients represent linear approximations to the known nonlinear relationships with copulations. We knew that male vis-

its was a consequence of female visits and a cause of disruptions, and no other variables seemed to determine male visits, so we proposed the causal chain relationship

$$\text{female visits} \rightarrow \text{male visits} \rightarrow \text{disruptions}$$

in the path diagram. The proposed computed correlation between female visits and disruptions ($0.931 \times 0.832 = 0.775$) is a reasonable

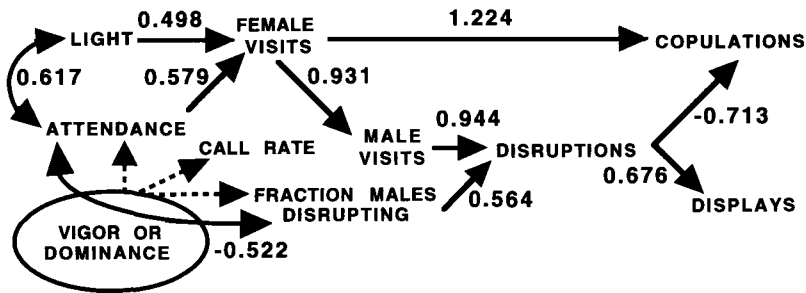


Fig. 7. Path diagram for most-parsimonious causal model of relationship of site characteristics, male behavioral characteristics, visits rates, and copulation success. Numbers are path coefficients. Single-headed straight arrows indicate proposed direct causes, and double-headed curved arrows indicate unanalyzed correlational effects. Effects of possible latent variable indicated in dashed lines.

prediction of the observed correlation (0.699). Next, we included the joint effect of attendance and light as determinants of female visits. A strong unanalyzed relationship between light and attendance (0.617) remained. This could have been due to a joint cause-and-effect relationship between attendance and female visits, but other explanations are possible. Finally, call rate appeared to be a correlate of attendance rather than a direct determinant of female visits as argued above, and displays appeared to be most strongly associated with disruptions. A model comprising only the variables light, attendance, female visits, male visits, disruptions, displays, and copulations explained 53.6% of the observed correlation among these variables.

The correlation matrix revealed several strong additional relationships. In particular, call rate was highly correlated with disruptions per male visitor, and both were correlated with attendance. Disruptions per male visitor was a reflection of a male's ability to repel intruders. By definition, the total number of disruptions was determined by the number of male visitors and the number of visiting males that were able to disrupt. We therefore added another path into the model between attendance and disruptions via disruptions per male. This required recomputing the path coefficients for disruptions using a multiple regression with male visits and disruptions per male. The link of attendance to disruptions per male is unanalyzed (-0.522), but we believe it may be the result of a latent (unmeasured) variable associated with the male's vigor, agility, and/or dominance. We have only suggested the existence of such a latent variable in the path diagram. The addition of this path into the model increases the explanatory power

of the overall model to 78.1% (using only correlations for the same pairs of variables analyzed in first model above). This path model represents the most-parsimonious explanation of the data. However, there is no statistical proof of its validity, and we regard it as an hypothesis for future experimental studies.

DISCUSSION

Male traits as cues for female choice.—We examined only a few of the possible male traits females might use to make mate choice decisions: number of calls, number of wing-snap displays, and attendance. Acoustic parameters of the sounds and the choreography of displays were not measured. Nevertheless, in a general search for all variables correlated with female visit rate, attendance was the one behavioral trait identified. Attendance is frequently found to be correlated with female visit rate and male mating success in many lek breeding species (e.g. Gibson and Bradbury 1985, Andersson 1989, Appolonio et al. 1989, Gibson et al. 1991, Hill 1991, Alatalo pers. comm.). Males must be present at their sites in order to mate, and they also must be present to defend their arenas against other males. In order to maintain a high presence level, males must forage very quickly, and it is possible that females could use attendance as an indicator of the male's foraging ability. Alternatively, males that are successful in attracting females because their sites are bright may be stimulated to spend more time at their arenas. Such an effect may be responsible for the large unexplained correlation between attendance and light quality of the site.

Calling by males on their arenas is clearly a

long-distance signal to attract females and fix the location of the male, but variation in calling rate was not associated with the ability to attract females in *Corapipo*. Although the top male did have the highest calling rate, Male 6 had a low calling rate but a high female visit rate, and Male 2 had a very high calling rate but a low female visit rate. Overall, the number of calls per hour was significantly correlated with attendance level, and even the calling rate per minute on the arena was correlated, although not quite significantly, with attendance. A positive correlation between vocalization rate and attendance has been found in several lek species and may reflect differences in male ability to invest time and energy in courtship (Vehrencamp et al. 1989).

Finally, the number of wing-snap displays was not at all correlated with female visit rate. This display, along with calling, display flights, and different movements on the log itself, has been described as courtship (Prum 1986). The successful male in our study always performed a single wing snap before copulation, but overall showed very low rates of wing-snapping. The same displays are also performed during male-male agonistic interactions. Repeated wing-snapping always was performed by arena owners while trying to repel intruders, as well as by intruding males. The frequency of wing-snap displays was best correlated with disruption rate. Wing-snapping rate could indicate to females the level of disruption they are likely to encounter at a site, but in fact it does not appear to deter female visits.

Site characteristics as cues for female choice.—The amount of sunlight falling on the display log, as estimated by our combined measure of mean light intensity and mean brightness contrast with the background, was strongly correlated with female visit rate. Similarly, on most arenas, females tended to visit only during those times of the day when gaps in the forest canopy permitted a sunbeam to hit the log. Females clearly prefer to visit and mate with males displaying at bright and contrasted sites, which determine the conspicuousness of the males' visual signals. A previous study showed that the structural shiny blue color of plumage on the upperparts can be observed only under conditions of direct sunlight (Théry 1990b). The striking movement of the courtship displays and the conspicuousness of the white color patches on a shiny blue plumage are enhanced by high

brightness contrast between the arena and the surrounding dark understory.

Thus, the pattern of light at arenas appears to be an important cue for mate choice in *C. gutturalis*. The structure of ornamental feathers, location of courtship arenas, and courtship postures also are related to light environments in other sympatric lekking manakins of French Guiana (Théry 1990b). No previous studies have analyzed the relationship between courtship behavior and light patterns on leks, but different authors have described arena locations related to forest openings (Diamond 1987, and references cited in Théry 1990b), active vegetation clearing by displaying males (LeCroy et al. 1980, LeCroy 1981, Borgia 1986, Beehler 1987, and references cited in Théry 1990b), and female preference for high-visibility mating sites (Deutsch and Weeks 1992).

Divergent observations have been reported on Guianan and Andean cocks-of-the-rock (*Rupicola rupicola* and *Rupicola peruviana*), close relatives of manakins. Gilliard (1962) noted in *R. rupicola* that sunlight stimulates display and suggested that light intensity on the forest floor may be important in the regulation of reproductive cycles, whereas in *R. peruviana*, Benalcazar and Benalcazar (1982) described males displaying under a light-intensity threshold to reduce the risk of predation. Light intensity has been suggested to determine display-site selection and lek position in the Mediterranean fruit fly (*Ceratitidis capitata*; Arita and Kaneshiro 1989), where males are detecting potential mates by the silhouette transmitted by sunlight through the upperpart of display leaves. As pointed out by Endler (e.g. 1992, 1993) the color of light also is very important in the ecology and evolution of animals, and perceived colors depend upon the interaction between ambient light color and the reflectance color of the animal part. Both the amount and color of light on the floor of tropical forests are extremely limited, and selection has favored the optimal use of the little that is there. Light quality at certain display hours may increase female crypsis and male conspicuousness, requiring measurements of birds and ambient light colors at display sites to test this hypothesis.

Male dominance-indicator model.—The male dominance-indicator model argues that females evolve preferences for certain male traits or for specific types of sites in order to obtain dominant males as mates. Dominant males are pre-

sumed to be higher-quality mates and females benefit by producing more viable offspring. A necessary (although not sufficient) condition for this hypothesis to be true is a correlation between the ability of males to dominate conspecific males and the trait or site cue preferred by females. In the Satin Bowerbird (*Ptilonorhynchus violaceus*; Borgia 1985a, b, Borgia and Gore 1986), well-constructed and highly decorated bowers are preferred by females. Males often destroy each others' bowers and steal decorations, which reduces the victim's mating success. Borgia argued that dominance at artificial feeding sites was related to success in protecting bowers, even though 94% of bower destruction occurred when the owner was away from his bower. In addition, only 17% of destructions were interrupted by returning owners, and the intruder was in most cases (60%) chased by the owner if present. The case for bower quality as an indicator of male dominance is at best weak (Wiley 1991), but bower quality certainly must be an indicator of the male's attendance level. A better case for dominance has been made for Black Grouse (*Lyrurus tetrix*), where males that are preferred by females over their immediate neighbors are those that can beat their neighbors in a staged fight on their territorial boundary (Alatalo et al. 1991).

Data from our study of *Corapipo* show that male dominance, as measured by the ability of log owners to repel intruding males in the presence of soliciting females, has a direct effect on male reproductive success. Similar direct effects of male interference have been found in other lekking piprids and cotingids (Lill 1974a, b, 1976, Foster 1983, Trail 1985a, b, McDonald 1989b, Trail 1990), also leading to a strong skew in male mating success in the Long-tailed Manakin, the Swallow-tailed Manakin (*Chiroxiphia caudata*), and the Capuchinbird (*Perissocephalus tricolor*). The question of interest is whether females use cues for mate choice that serve as indirect measures of male dominance. Our analysis suggests the possibility that a latent variable, such as male vigor or foraging ability, underlies a male's ability to both repel intruders and attend/call at high rates. Attendance, therefore, could provide some information on male dominance as well as quality. However, there is no correlation between a male's ability to prevent disruptions and the light quality of his site, suggesting that dominant males cannot acquire the arenas most preferred by females. A possible reason for this

may be that the presence of sun patches on logs changes more rapidly with the growth and loss of canopy vegetation than the turnover of male log ownership.

In conclusion, the light environment at the display arena of male *Corapipo* appears as the primary determinant of female visit rate and, therefore, the main cue females use in selecting mates. However, a large fraction of mountings are interrupted and the mating success of males is greatly modulated by their ability to repel intruding males during copulation attempts. Males must both possess a bright site and dominate their neighbors in order to copulate successfully. Females mate with dominant males in the end, but dominance does not appear to be a trait particularly sought by females in their initial choice of mates.

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LITERATURE CITED

- ALATALO, R. V., J. HÖGLUND, AND A. LUNDBERG. 1991. Lekking in the Black Grouse—A test of male viability. *Nature* 352:115–156.
- ANDERSSON, S. 1989. Sexual selection and cues for female choice in leks of Jackson's Widowbird *Euplectes jacksoni*. *Behav. Ecol. Sociobiol.* 25:403–410.
- APPOLONIO, M., M. FESTA-BIANCHET, AND F. MARI. 1989. Correlates of copulatory success in a fallow deer lek. *Behav. Ecol. Sociobiol.* 25:89–97.
- ARITA, L. H., AND K. Y. KANESHIRO. 1989. Sexual selection and lek behavior in the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). *Pacif. Sci.* 43:135–143.
- BALMFORD, A. 1991. Mate choice on leks. *Trends Ecol. & Evol.* 6:87–92.
- BEEHLER, B. M. 1987. Ecology and behavior of the Buff-tailed Sicklebill (Paradisaeidae: *Epimachus albertisi*). *Auk* 104:48–55.
- BEEHLER, B. M., AND M. S. FOSTER. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. *Am. Nat.* 131:203–219.

- BENALCAZAR, C. E., AND F. S. BENALCAZAR. 1982. Display of the Andean Cock-of-the-rock. Pages 178-181 in *The cotingas* (D. W. Snow, Ed.). British Museum (Natural History), London, and Oxford Univ. Press, Oxford.
- BORGIA, G. 1979. Sexual selection and the evolution of mating systems. Pages 19-80 in *Sexual selection and the evolution of mating systems in insects* (M. Blum and A. Blum, Eds.). Academic Press, New York.
- BORGIA, G. 1985a. Bower quality, number of decorations, and mating success of male Satin Bowerbirds (*Ptilonorhynchus violaceus*): An experimental analysis. *Anim. Behav.* 33:266-271.
- BORGIA, G. 1985b. Bower destruction and sexual competition in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Behav. Ecol. Sociobiol.* 18:91-100.
- BORGIA, G. 1986. Sexual selection in bowerbirds. *Sci. Am.* 254(6):92-101.
- BORGIA, G., AND M. A. GORE. 1986. Feather stealing in the Satin Bowerbird (*Ptilonorhynchus violaceus*): Male competition and the quality of display. *Anim. Behav.* 34:727-738.
- BRADBURY, J. W. 1977. Lek mating behavior in the hammer-headed bat. *Z. Tierpsychol.* 45:225-255.
- BRADBURY, J. W. 1981. The evolution of leks. Pages 138-169 in *Evolution of social behavior: Hypotheses and empirical tests* (R. D. Alexander and D. Tinkle, Eds.). Chiron Press, New York.
- BRADBURY, J. W., AND R. M. GIBSON. 1983. Leks and mate choice. Pages 109-138 in *Mate choice* (P. Bateson, Ed.). Cambridge Univ. Press, Cambridge.
- BRADBURY, J. W., R. M. GIBSON, AND I. M. TSAI. 1986. Hotspots and the evolution of leks. *Anim. Behav.* 34:1694-1709.
- BRADBURY, J. W., S. L. VEHCAMP, AND R. M. GIBSON. 1985. Leks and the unanimity of female choice. Pages 301-314 in *Evolution, essays in honour of John Maynard Smith* (P. J. Greenwood, P. H. Harvey, and M. Slatkin, Eds.). Cambridge Univ. Press, Cambridge.
- DEUTSCH, J. C., AND P. WEEKS. 1992. Uganda kob prefer high-visibility leks and territories. *Behav. Ecol.* 3:223-233.
- DIAMOND, J. 1987. Bower building and decoration by the bowerbird *Amblyornis inornatus*. *Ethology* 74:177-204.
- ENDLER, J. A. 1992. Signals, signal conditions and the direction of evolution. *Am. Nat.* 139:S125-S153.
- ENDLER, J. A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* 63:1-27.
- ERARD, C., M. THÉRY, AND D. SABATIER. 1989. Régime alimentaire de *Rupicola rupicola* (Cotingidae) en Guyane Française, relations avec la frugivorie et la zoochorie. *Rev. Ecol. (Terre Vie)* 44:47-74.
- FOSTER, M. S. 1983. Disruption, dispersion, and dominance in lek-breeding birds. *Am. Nat.* 122:53-72.
- GIBSON, R. M., AND J. W. BRADBURY. 1985. Sexual selection in lekking Sage Grouse: Phenotypic correlates of male mating success. *Behav. Ecol. Sociobiol.* 18:117-123.
- GIBSON, R. M., J. W. BRADBURY, AND S. L. VEHCAMP. 1991. Mate choice in lekking Sage Grouse revisited: The roles of vocal display, female site fidelity, and copying. *Behav. Ecol.* 2:165-180.
- GILLIARD, E. T. 1962. On the breeding behavior of the Cock-of-the-rock (*Aves, Rupicola rupicola*). *Bull. Am. Mus. Nat. Hist.* 124:31-68.
- HILL, W. L. 1991. Correlates of male mating success in the Ruff *Philomachus pugnax*, a lekking shorebird. *Behav. Ecol. Sociobiol.* 29:367-372.
- JULLIOT, C., AND D. SABATIER. 1993. Diet of the red howler monkey (*Allouata seniculus*) in French Guiana. *Int. J. Primatol.* 14:527-550.
- LECROY, M. 1981. The genus *Paradisaea*—Display and evolution. *Am. Mus. Novit.* 2714.
- LECROY, M., A. KULUPI, AND W. S. PECKOVER. 1980. Goldie's Bird of Paradise: Display, natural history and traditional relationships of people to the bird. *Wilson Bull.* 92:289-301.
- LI, C. C. 1986. Path analysis: A primer, 4th ed. Boxwood Press, Pacific Grove, California.
- LILL, A. 1974a. Sexual behavior in the lek-forming White-bearded Manakin, *M. manacus trinitatis* Hartert. *Z. Tierpsychol.* 36:1-36.
- LILL, A. 1974b. Social organization and space utilization in the lek-forming White-bearded Manakin, *M. manacus trinitatis*. *Z. Tierpsychol.* 36:513-530.
- LILL, A. 1976. Lek behavior in the Golden-headed Manakin (*Pipra erythrocephala*) in Trinidad (West Indies). *Z. Tierpsychol. Suppl.* 18.
- LYTHGOE, J. N. 1979. The ecology of vision. Oxford Univ. Press, Oxford.
- MCDONALD, D. B. 1989a. Correlates of male mating success in a lekking bird with male-male cooperation. *Anim. Behav.* 37:1007-1022.
- MCDONALD, D. B. 1989b. Cooperation under sexual selection: Age-graded changes in a lekking bird. *Am. Nat.* 134:709-730.
- ORING, L. W. 1982. Avian mating systems. Pages 1-92 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King and K. Parkes, Eds.). Academic Press, New York.
- PRUM, R. O. 1986. The displays of the White-throated Manakin *Corapipo gutturalis* in Suriname. *Ibis* 128:91-102.
- SNOW, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis* 112:299-329.
- THÉRY, M. 1987. Influence des caractéristiques lumineuses sur la localisation des sites traditionnels, parade et baignade des manakins (Passeriformes, Pipridae). *C. R. Acad. Sci. Paris, Sér. III* 304:19-24.

- THÉRY, M. 1990a. Display repertoire and social organization of the White-fronted and White-throated manakins. *Wilson Bull.* 102:123-130.
- THÉRY, M. 1990b. Influence de la lumière sur le choix de l'habitat et le comportement sexuel des Pipridae (Aves: Passeriformes) en Guyane Française. *Rev. Ecol. (Terre Vie)* 45:215-236.
- THÉRY, M. 1992. The evolution of leks through female choice: Differential clustering and space utilization in six sympatric manakins. *Behav. Ecol. Sociobiol.* 30:227-237.
- TRAIL, P. W. 1985a. Courtship disruption modifies mate choice in a lek-breeding bird. *Science* 227:778-780.
- TRAIL, P. W. 1985b. Territoriality and dominance in the lek-breeding Guianan Cock-of-the-rock. *Natl. Geogr. Res.* 1:112-123.
- TRAIL, P. W. 1990. Why should lek-breeders be monomorphic? *Evolution* 44:1837-1852.
- VEHRENCAMP, S. L., J. W. BRADBURY, AND R. M. GIBSON. 1989. The energetic cost of display in male Sage Grouse. *Anim. Behav.* 38:885-896.
- WILEY, R. H. 1991. Lekking in birds and mammals: Behavioral and evolutionary issues. *Adv. Stud. Behav.* 20:201-291.
- WOOTTON, J. T. 1994. Predicting direct and indirect effects: An integrated approach using experiments and path analysis. *Ecology* 75:151-165.
- WRIGHT, S. 1934. The method of path coefficients. *Ann. Math. Stat.* 5:161-215.