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Manakin display and visiting behaviour: a comparative test of sensory drive

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The conspicuousness of bird plumages may vary with the ambient light. Therefore, two behavioural predictions of the sensory drive hypothesis are that males should prefer to display and that females should prefer to visit males under specific ambient light conditions that enhance communication efficiency. Here we investigate patterns of male display and female attendance at male display sites under different ambient light conditions in a clade of five closely related species of manakins (Pipridae). Continuous focal observations and video recordings showed that in four of five species, the frequency of male display in different ambient light conditions correlated with their availability at their display sites, and that males showed no preference for displaying under specific ambient light conditions. But in *Corapipo gutturalis*, males showed a strong preference for displaying in shade and sunny gap environments. Females showed no preference for visiting male display sites under specific ambient light conditions, nor did they prefer males with the strongest ambient light display preferences. Male display and female visiting patterns for most of the manakin species studied were inconsistent with behavioural predictions of sensory drive. However, male *C. gutturalis* have evolved a preference for displaying in specific light conditions that is a derived behaviour novelty within the clade. As predicted by sensory drive, this behavioural novelty is phylogenetically congruent with a change in sensory environment: a decrease in the frequency of cloudy conditions at display sites. Behavioural and environmental novelties in *C. gutturalis* are not phylogenetically congruent with the evolution of the glossy, blue-black and white plumage in the ancestor of all *Corapipo*. Further tests of the sensory drive hypotheses are recommended, such as whether display sites are nonrandom samples of the sensory environment or whether male plumage colours are adapted for efficient signalling in specific ambient light conditions.

Keywords: display behaviour; female visting rate; manakin; Pipridae; sensory drive

Manakins (Pipridae) are highly polygynous birds restricted to Neotropical forest habitats (Snow 1963; Sick 1967; Prum 1990). In most species, males aggregate in leks, which females visit to choose mates; males contribute solely sperm for reproduction (Bradbury & Gibson 1983; Andersson 1994). As a result of strong intersexual selection, males have diverse bright plumages and perform elaborate courtship displays (Prum 1990). Several mechanisms of sexual selection by female choice have been suggested for the evolution of courtship displays and other secondary sex ornaments in polygynous clades (e.g. quality indicator, Fisherian arbitrary selection, sensory bias; review in Andersson 1994; Prum 1997). Recently, the sensory drive mechanism has been hypothesized to be important in the evolution of manakin display behaviour and plumage colour (Théry & Vehrencamp 1995; Endler & Théry 1996; Heindl & Winkler 2003a, b; Uy & Endler 2004).

The sensory drive mechanism hypothesizes that natural selection on female mating preferences favours the evolution of conspicuous male displays, which communicate efficiently to the female sensory system and lower mate search costs (Endler & McLellan 1988; Ryan 1990; Endler

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1992; Endler & Basolo 1998). Plumages and display behaviours vary in signalling properties with the ambient light (i.e. light available in the habitat as a combination of forest geometry and weather, Endler 1993), such that the conspicuousness of visual signals may vary under differing illumination conditions (e.g. Théry & Vehrencamp 1995; Endler & Théry 1996). Unlike other sexual selection models, sensory drive predicts that in the absence of evolution of the females' sensory system, phylogenetic changes in male plumage signals and displays should correspond to changes in the light environment (e.g. Shaw 1995; Prum 1997).

Sensory drive may select on many aspects of male display phenotype. Given that many males display from established sites within territories, an ancillary behavioural prediction of sensory drive is that males may evolve preferences for displaying under specific ambient light conditions that promote signal efficiency, and that females should prefer to visit males under the same ambient light conditions. It is conceivable that male signals could evolve by sensory drive without the evolution of male behavioural preferences to display under the most efficient light environments. However, it is unlikely that sensory drive could play a strong role in sexual selection if females do not prefer to search for mates under the most efficient signalling conditions (if such exist).

Ultimately, understanding the role of the sensory drive mechanism in the evolution and diversification of secondary sexual characters will require not merely examining the correlation between signals and environments, but also investigating whether phylogenetic patterns in signal phenotype evolution match comparative variation in the sensory enviornment (Prum 1997; Endler & Basolo 1998). In this and future papers, we attempt to test behavioural and plumage colour predictions of sensory drive in a polygynous clade of manakins.

The manakin tribe Ilicurinii is a clade containing the genera *Corapipo*, *Masius* and *Ilicura*, which show highly complex patterns of similarity of display behaviour (Prum 1990, 1992, 1997). Birds in this clade display on mossy fallen logs or in horizontal branches and their courtship behaviours have been described in some detail (Skutch 1967; Snow & Snow 1985, 1992; Prum 1986; Prum & Johnson 1987). A phylogenetic hypothesis is available for the family, and analysis of plumage and display evolution indicate that species share a variety of behavioural elements but each has unique features (Prum 1990, 1992, 1997). Furthermore, species in this group occupy distinct geographical ranges (Ridgely & Tudor 1994) and their habitats are probably variable in ambient light conditions because of variation in forest structure and climate (Théry 2001). Previous studies of *Corapipo gutturalis* suggest that females rely on the visual contrast during male courtship to choose their mates (Endler & Théry 1996).

As part of comparative investigation of the role of sensory environment in the diversification of secondary sexual traits, we studied the light environments used during polygynous courtship display in the *Ilicura–Corapipo* clade. Considering that there are temporal changes in the illuminating conditions of male display perches, we tested whether display behaviour changes with temporal changes in light conditions. Specifically, we test the behavioural prediction that individual males will prefer to display at their display sites under a subset of the light conditions available to promote signalling efficiency. For this, we compared the display activity of males during the different classes of available ambient light conditions at established display sites of five species in the *Ilicura–Corapipo* clade. Each male displays primarily from one location, or a few similarly lit locations within its lek territory. During the course of a day, the ambient light conditions at that display site will change because of the presence or absence of clouds, the movement of the sun, and the distribution of vegetation around the display site. We examined whether the rate of male display changes with these temporal changes in ambient lighting of the display perch and whether female visiting rates similarly change with ambient illumination of the display perch. We also compared female visiting rates with the degree of males' preference for displaying under a subset of the available light environments in four of the five species.

The analyses presented here test an important prediction of the sensory drive mechanism of sexual selection, and further tests of the hypothesis are encouraged to test, for example, whether display sites are nonrandom samples of the sensory environment, or whether male plumage colours are adapted for efficient signalling in specific ambient light conditions.

METHODS

Study Localities and Display Sites

Fieldwork was conducted between November 2000 and July 2003 at five field sites in Costa Rica, Ecuador and Brazil (Table 1). Observations were made for ca. 20 days during the breeding season for each population. Males were observed at three to 30 display sites, used by one to 17 individuals, distributed in one to seven leks sampled by species, totalizing 6787, 5-min intervals (ca. 567 h) of continuous focal observations (Table 1). Display sites consisted of fallen mossy logs in *Corapipo* and *Masius*, buttress roots in *Masius* and *Ilicura* and tree branches in *Ilicura*. In all species except *Ilicura militaris*, display sites were on the forest ground, whereas in *I. militaris*, males displayed on perches on the ground and up to about 20 m high (two cases), and sampling on this species was limited to display sites lower than 8 m.

In *Corapipo* and *Masius*, each individual male predominantly used one display log within a territory of ca. 30 m in diameter. In a few cases (one male in *Corapipo gutturalis*, *C. altera* and *Masius chrysopterus*; two in *C. heteroleuca*), males used two to four logs within their territories. In *Ilicura*, four of the 17 males sampled used multiple display perches (from two to seven) within a territory of ca. 40 m in diameter (the exceptional individual using seven display perches held a territory of ca. 60 m in diameter). In all these cases, males used mostly one of the display perches during the observations of a day, and the data for the additional perches

Table 1. Study sites, sampling efforts and sample sizes of behavioural observations conducted for the studied populations

						Behavioural observations				
Taxa	Locality	County	Province	Country	Geographical coordinates	Hours	Leks	DS	Individuals	% *d*
C. altera	Pocosol	La Tigra	Puntarenas	Costa Rica	10°22′ N; 84°37′ W	45	1	3	1	57.06
C. heteroleuca	Las Cruces	San Vito	Puntarenas	Costa Rica	08°47′ N; 82°58′ W	110	5	12	10	73.75
C. gutturalis	Dimona	Manaus	Amazonas	Brazil	02°20′ S; 60°05′ W					
C. gutturalis	Km 41 BR 170	Manaus	Amazonas	Brazil	02°26′ S; 59°45′ W	186	7	14	11	43.42
M. c. coronolatus	Tandayapa	Nanegalito	Pichincha	Ecuador	00°01′ S; 78°46′ W					
M. chrysopterus	Sumaco	Sumaco	Napo	Ecuador	00°34′ S; 77°38′ W	140	2	6	4	20.89
I. militaris	Serra do Brigadeiro	Ervalia	Minas Gerais	Brazil	19°56′ S; 43°56′ W					
I. militaris	Barreiro	Belo Horizonte	Minas Gerais	Brazil	21°40′ S; 42°31′ W	85	4	30	17	76.06

DS = display sites; % *d* = frequency of displays for all individuals (% of 5-min periods of observation with some physical display). Data from different populations of *C. gutturalis*, *M. chrysopterus* and *I. militaris* were grouped, as no significant differences in behaviour were found among them.

were collected on separate days and pooled by individual. In the only two cases in which a single male was observed using multiple perches during sampling, the ambient light condition remained the same for all perches (i.e. one day in *C. heteroleuca* under a cloudy environment and one day in *I. militaris* under shade light). Observations on territoriality were confirmed by colour banding of individuals captured in mist-nets in the last week of fieldwork at each locality (permits issued to M.A. by respective federal agencies).

Behavioural Sampling

Display sites were searched for from early morning to dusk through continuous acoustic and visual censuses. Once display sites were located, male territories were mapped with GPS. Territory attendance, song, display behaviour and social interactions were sampled by continuous focal observations (Altman 1974) with frequency data recorded for every 5-min interval. Observations and video recordings (with a Sony DCR-VX 2000 camera) were conducted behind a camouflaged blind located usually 10 m from the focal display site, and each display site was sampled for up to 5 nonconsecutive days. Irradiance spectra of the environmental light were taken simultaneously during the behavioural observations with an Ocean Optics spectrophotometer and a 10-m-long optic fibre with a cosine corrector placed exactly next to the display perch. These spectral data will be presented elsewhere. There was no indication that the blind, video recording or the spectrophotometer probe interfered with the birds' behaviour.

Light Categories

During each 5-min observation period, the ambient light incident on the display perch of the focal male was classified into one of three categories based on visual observation, which were confirmed by spectral measurements (not analysed here).

If light conditions varied within the 5-min period, ambient light was classified according to the most frequent light available at the focal display site during the observation.

The three classes of ambient light were (1) cloudy: when the sun was obstructed by clouds; (2) shade: when most of the sunlight reaching the display site was filtered by vegetation (equivalent to forest shade of Endler 1993); and (3) sunny gap: when most of the sunlight reached the display site directly.

When both shade and sunny gap environments were available on the display log at the same time, light was classified according to the predominant light available (i.e. shade or sunny gap). Mixed shade/sunny gap light was observed in 8.4% of the observation periods in *C. gutturalis*, and these conditions were also analysed separately from shade and sunny conditions in this species (see below). This condition was observed only in one 5-min period in *C. heteroleuca* and, in the other species, display sites were exposed to one predominant class of ambient light at all times.

Data Analysis

Light availability is defined as the frequency distribution of the three classes of ambient light for each individual male or species at the focal display sites. The observed display frequencies are the percentages of observation intervals (5-min period) with some display activity. Behavioural preferences for specific ambient light conditions were examined by comparing the observed display frequencies under each class of ambient light with the expected frequencies given by the frequency of each ambient light for each population and each individual using *G* tests. The *G* statistic tests for the association of display behaviour and ambient light for the population as a whole (pooled data) and for each individual. The *G* test also estimates the significance of the individual heterogeneity component of variance in the data, to assess the among individual variation in the association between behaviour and ambient light. Fisher's exact test was also used when frequencies from individual data were small (<3). Individuals tested through Fisher statistics were not included in the *G* tests of heterogeneity of a population. In *C. gutturalis,* the pooled data for the whole population was also analysed to test for differences in display behaviour under mixed shade/sunny gap in comparison with periods of shade or sunny gap conditions. The display behaviour under shade and sunny gap light when both conditions were available (mixed shade/sunny gap) was also compared in this species.

Because most males of all species displayed predominantly at one log or perch, and those that used multiple logs or perches experienced uniform ambient light conditions among perches during the observations, this analysis focuses on whether males choose to display under a single available light condition, and not whether they behaviourally choose among different lighting conditions available at different locations at the same time.

To assess whether display vigour varied among classes of ambient light, we also compared the frequency of displays (i.e. proportion of displays under each ambient light category) and display rate (i.e. number of behavioural elements per minute when present) among the available classes of ambient light with the frequency of occurrence of each class of ambient light through multivariate analysis of variance (MANOVA), with ambient light as multiple dependent variables.

Female visiting was analysed only for the four species in which more than eight female visits were observed: *I. militaris*, *C. heteroleuca*, *C. altera* and *C. gutturalis*. Green plumaged birds in a male territory which did not display courtship behaviour or aggression were identified as visiting females (Prum 1986; Prum & Johnson 1987). Observations of males in predefinitive, green plumages displaying alone or together with territorial males were frequent. Only three out of 77 female visits culminated in copulation.

Female preferences for visiting males under specific classes of ambient light were assessed by comparing the frequency of female visits (i.e. the proportion of visits during each light class) to male territories during each ambient light category with the frequency distribution of the available ambient light, through chi-squared and Fisher's exact tests. To examine whether females visited more frequently those males that showed the strongest individual preferences for specific ambient light conditions, we correlated the coefficient of variation in male display frequencies (proportion of the displays under each light class) with the rate of female visits per hour. To examine whether females preferred the most active males, we also correlated male display rate (number of behavioural elements per min when present) to the rate of female visits per hour. Because only one male *C. altera* was observed, the species was not included in these analyses.

RESULTS

During the entire study, 48 (74%) of the observed display sites received all three light types. Availability of the three major categories of ambient light was generally homogeneous among individual territories within populations, with a few exceptions. In *C. gutturalis*, cloudy conditions were not available for two of the 11 individuals studied, and sunny gaps were not available for one individual. In *I. militaris*, cloudy conditions were the only ambient light available for three of the 17 studied individuals, and seven others did not have sunny gaps available. In four species, cloudy conditions were most frequent, varying from 80% (±0.02) in *M. chrysopterus* to 56% in *C. altera* (Fig. 1a). In contrast, shade conditions were the most frequently available in *C. gutturalis* (mean + $\mathrm{SE} = 72 + 0.02\%$; Fig. 1a).

In four out of five species examined, males showed no preference for displaying under any specific ambient light conditions; rather, males displayed in each class of ambient light with the same frequency as its frequency of occurrence ($G_2 < 2.58$, $P > 0.11$; Fig. 1a). In all species that showed no ambient light preference, the most common ambient light condition was cloudy. In contrast, male *C. gutturalis* preferred to display under shade and sunny gap conditions (i.e. noncloudy conditions; Fig. 1a; $G_2 = 43.49$, $P < 0.01$), but display frequencies were not significantly different between shade and sunny gap light environments ($\chi^2_1 = 0.07$, $P = 0.79$). The frequency of displays in *C. gutturalis* was also not different between shade environments and mixed shade/sunny gap environments ($\chi^2_1 = 2.27$, $P = 0.13$), but both were preferred over cloudy conditions ($G_2 = 24.35$, $P < 0.05$). Under the mixed light condition available for *C. gutturalis*, males did not show preference for displaying under the shade or sunny gap light ($G_1 = 1.49$, $P = 0.22$).

Within all species (except *C. altera*, $N = 1$), some individuals preferred to display in particular classes of ambient light. The single male *C. altera* observed did not show a preference for any ambient light class (Table 2). *Corapipo gutturalis* and *I. militaris* included both selective and nonselective males. *Corapipo gutturalis* showed the highest proportion of individual males preferring particular classes of ambient light, and therefore the component of total variance in preference for light environments was also significant in this species. Some males of *C. gutturalis* preferred displaying during intervals of either shade or sunny gaps equally, but other males specifically preferred periods of pure shade. The variation among individuals and the component of total variance in preference for light environments were also high in *I. militaris*, but not in *C. heteroleuca* or *M. chrysopterus*.

The proportion of the observed displays in each ambient light category was significantly different among the available ambient light categories, and varied accordingly to the availability of ambient light, for all studied populations (Fig. 1a, Table 3). The rate of display (i.e. the number of displays observed per min when the bird was present in the territory), however, was only significantly different among different classes of ambient light in *C. gutturalis*, in which males displayed at increased rates

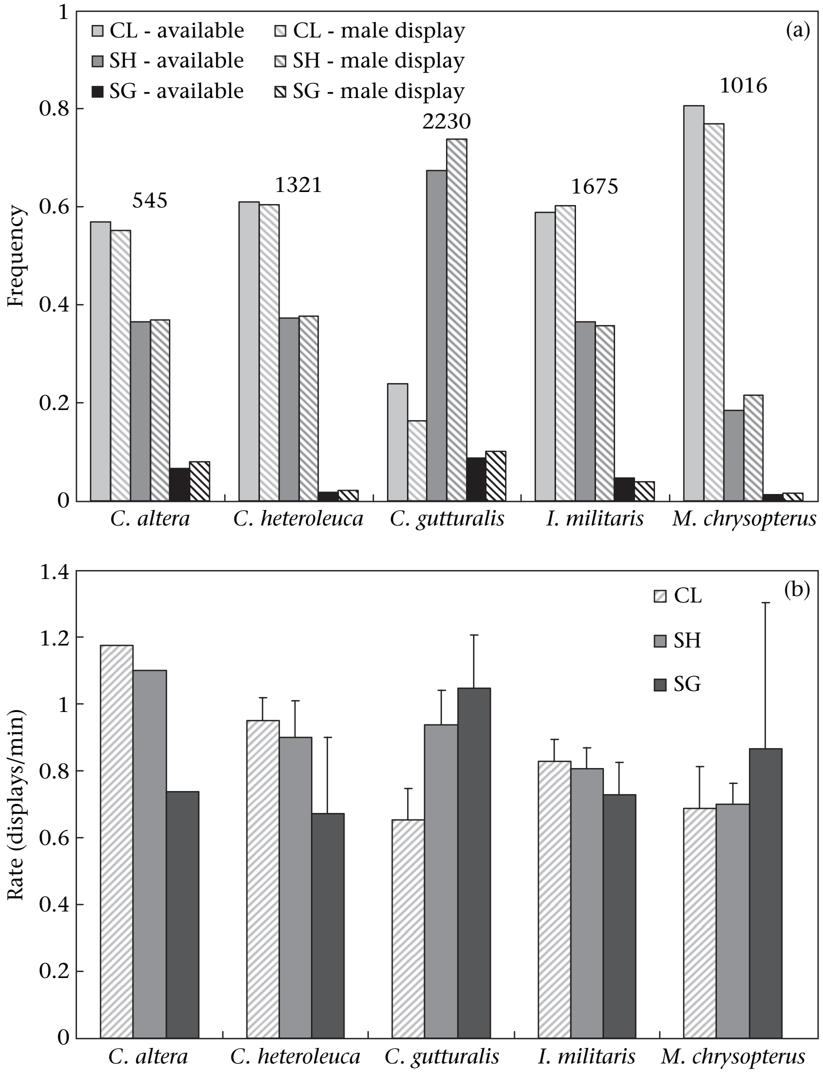

Figure 1. (a) Comparison of the frequency of available classes of ambient light, and the frequency of male display during each class of light (i.e. proportion of displays under each ambient light category) at display sites for five manakin species. CL = cloudy; SH = shade; SG = sunny gap. Sample sizes (number of observed intervals per species) are shown above bars, and total display frequencies are given in Table 1. (b) Mean display rate (±SE) of individuals under each ambient light. Only intervals when the focal male was present on the territory were considered. CL = cloudy; SH = vegetation shade; SG = sunny gap.

when sunny gaps illuminated the display perches (Fig. 1b, Table 3).

For the four species with a sufficient number of female visits to analyse, the observed frequencies of female visits during each ambient light class were not significantly different from a random expectation (all Fisher's exact tests, $Z_1 < 1.32$, $P > 0.23$; Fig. 2). Furthermore, in none of the three species with sufficient samples of both males and female visits did females more frequently visit males with stronger preferences for specific ambient light conditions, measured as the coefficient of variation in display frequencies among ambient light categories (all Spearman correlations: $r < 0.35$, $P > 0.17$; Fig. 3a). Although most male *C. gutturalis* preferred to display in shade and sunny gaps (Table 2), female visits were not correlated to the magnitude of ambient light preference of individual males. Finally, there was a trend towards increased female visits with increasing total male display rate in *C. heteroleuca* and *I. militaris*, but not in *C. gutturalis* (Fig. 3b), although the association was not statistically significant in any species (Spearman correlation: *C. heteroleuca* $r = 0.56$, $P = 0.09$; *I. militaris* $r = 0.36$, $P = 0.17$; *C. gutturalis* $r = -0.07$, $P = 0.83$).

DISCUSSION

If natural selection acts on female mating preferences to maximize sensory efficiency, females should prefer to visit male display sites under those ambient light conditions that promote signalling efficiency. An ancillary behavioural prediction of this sensory drive mechanism is that males may evolve preferences for displaying under the most efficient ambient light conditions as a result of female choice. Our results show that males of four of five species within a clade of manakins do not show

Table 2. Results of *G* and Fisher's exact tests for the association between the available ambient lights and male display behaviour

Species	GT	GP	GH	*nG*	*n* tested	Preferred AL (*n*)	*n* not tested (AL)	% Indv/AL	*Tn*
Corapipo altera	0.26	—	—	1	1	—	—	—	1
Corapipo heteroleuca	11.97	0.33	11.64	10	10	CL (1)	—	0.10	10
Corapipo gutturalis	64.89**	43.49**	21.39*	9	9	SH and SG (5)	1 (SH); 1 (SG)	0.56	11
Masius chrysopterus	6.24	2.58	3.66	3	3	VS (1)	—	0.33	3
Ilicura militaris	17.03*	2.29	14.74*	7	14	CL (1)	3 (CL)	0.07	17

Significances are shown for the following: GT = total variance in behaviour due to the individual *G* values; GP = variance in behaviour due to the pooled individual data; GH = variance in behaviour due to the heterogeneity among individuals; and *nG* = number of individuals included in the *G* tests for each population; *n* tested = total number of individuals tested with *G* and Fisher's exact tests; preferred AL = preferred classes of ambient light with number of individuals in parentheses, CL = cloudy, VS = shade, SG = sunny gap; *n* not tested = individuals observed on a single class of ambient light; % indv/AL = proportion of individuals showing a preference to display in particular classes of ambient light, in each population; *T* = total number of sampled individuals. *$P < 0.05$; **$P < 0.01$.

a preference for displaying under any specific ambient light condition. Rather, they display in the different ambient light conditions in the same frequency as their availability at their display sites. However, male *C. gutturalis* preferred to display under a subset of the light conditions available at their display sites: shade and sunny gaps. In other words, male *C. gutturalis* significantly avoided displaying under cloudy conditions, but did not show a significant preference for either shade or sunny gap conditions. These results corroborate the observations of Endler & Théry (1996) that male *C. gutturalis* display most frequently in noncloudy conditions.

Individual male *C. gutturalis* and *I. militaris* varied significantly among each other in their ambient light preferences (Table 2). Interestingly, significant variation among males in their preferences for different classes of ambient light indicates either (1) that male ambient light preferences are not under strong directional or purifying intersexual selection, or (2) that male preferences are not heritable and cannot respond to selection. In any case, the existence of significant variation in strength and heterogeneity in direction of ambient light preferences among males does not support the sensory drive hypothesis.

In none of the three species with sufficient number of males and female visits to analyse did females show a significant preference to visit male display sites under specific ambient light conditions. These results contradict a primary prediction of the sensory drive hypothesis. Furthermore, females of these three species did not prefer to visit males showing the strongest ambient light preferences or with the greatest rate of display behaviour. This was particularly noticeable for *C. gutturalis*, in which males displayed at higher rates under sunny gap environments.

Since *C. gutturalis* is not the basal lineage within this clade (Prum 1990, 1997), its unique behavioural preference for shade and sunny gap light conditions is an autapomorphy (i.e. a unique derived character) of this species (Fig. 4). As predicted by sensory drive, this derived behavioural preference is phylogenetically associated with a derived change in sensory environment (Prum 1997; Endler & Basolo 1998). *Corapipo gutturalis* was the only species in the clade for which noncloudy conditions were the most common ambient light available at their display sites (Fig. 1a). It is possible that the derived behavioural preference of *C. gutturalis* for noncloudy conditions evolved in response to a change in the predominant ambient light environment from the plesiomorphic (i.e. primitive), cloud-dominant light conditions found during the breeding season at display sites in all other species in the clade. *Corapipo gutturalis* is broadly distributed in the rain forests of Guianan South America above 250 m, whereas the other species of *Corapipo* and *Masius* are found breeding in upper montane 'cloud forests' of Central America and the Andes above 400 m (Stiles & Skutch 1989; Ridgely & Tudor 1994). Results from ecological niche modelling based on climatic and topographic data indicate that, in fact, *C. gutturalis* has a derived niche within the clade, converging in niche space on other manakins distributed in lowland forests (Anciães 2005; M. Anciães & A. T. Peterson, unpublished data).

Interestingly, however, the derived ambient light preference in male *C. gutturalis* is not phylogenetically coincident with major phenotypic changes in plumage colour. All species of monophyletic genus *Corapipo* are characterized by glossy blue-black body plumage and a white throat patch that evolved in the common ancestor of *Corapipo*

Table 3. Summary of multiple analysis of variance for the frequency (proportion of observation intervals) and rate (number of behavioural elements per minute) of male displays under the available classes of ambient light

Species	Display frequency	Rao *R* (df)^{P}	Display rate	Rao *R* (df)^{P}	Availability	Rao *R* (df)^{P}
Corapipo altera	CL	—	—	—	CL	—
Corapipo heteroleuca	CL	2054.70 (2,8)**	—	0.96 (2,5)	CL	2071.06 (2,8)**
Corapipo gutturalis	VS	51.88 (2,9)**	SG	7.43 (2,5)*	VS	82.18 (2,9)**
Ilicura militaris	CL	99.88 (2,15)**	—	1.16 (2,8)	CL	60.14 (2,15)**
Masius chrysopterus	CL	3326.73 (2,1)*	—	0.08 (2,2)	CL	1176.12 (2,1)*

Classes of ambient light with significantly higher values are shown. *$P < 0.05$; **$P < 0.01$.

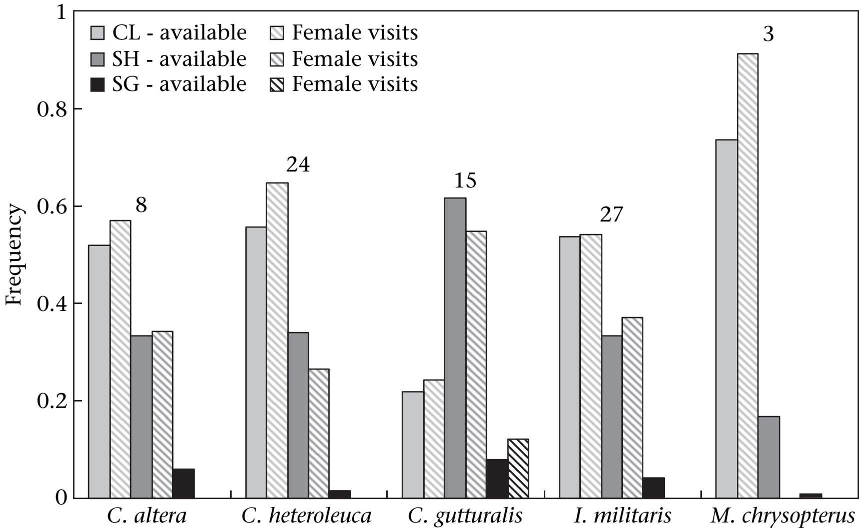

Figure 2. Observed frequencies of each class of ambient light and the frequency of female visits to male displays under that class of light (all Fisher's exact test comparisons, not significant). CL = cloudy; SH = shade; SG = sunny gap. Total number of observation intervals with female visits per species is indicated above bars.

(Prum 1997; Fig. 4). Endler & Théry (1996) hypothesized that the blue-black and white plumage of *C. gutturalis* maximizes brightness contrast under its preferred sunny gap and shade light conditions. However, our results imply that this contrasting *Corapipo* plumage pattern did not evolve for that sensory function, because the other closely related *Corapipo* species that share this general plumage pattern show no behavioural preference for sunny gap or shade conditions (Fig. 1a). In a phylogenetic context, the contrasting blue-black and white plumage is an exaptation for this contrasting visual sensory function, not an adaptation for it.

Further researches aiming to test other fundamental predictions of the sensory drive model are needed, specifically concerning whether display sites are a nonrandom sample of the entire sensory environment available in the habitat, or whether male plumage colours are adapted for efficient signalling in the specific ambient light conditions. Ultimately, understanding the role of the sensory drive mechanism in the evolution and

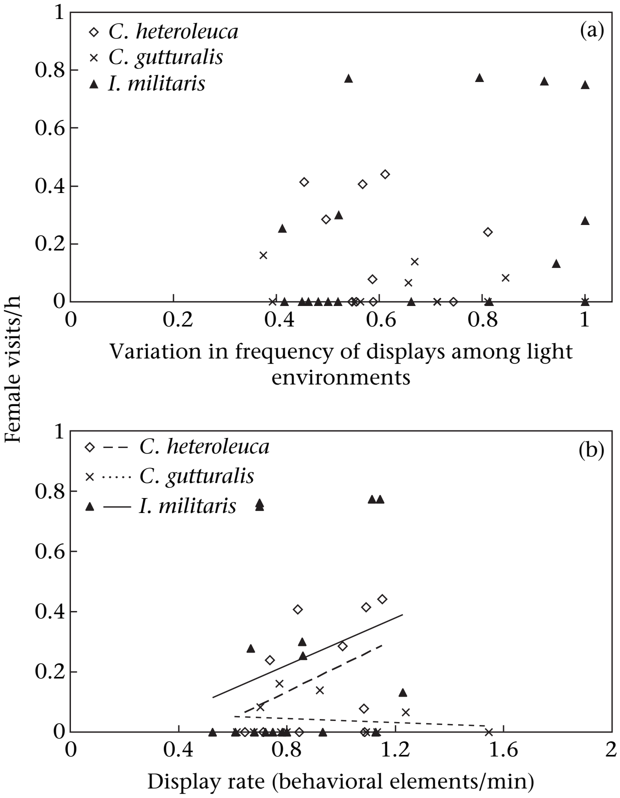

Figure 3. Variation in female visits among males in relation to the (a) strength of male preference to display during a specific class of ambient light (given by the coefficient of variation in display frequency among light environments), and (b) display rate (display elements/min).

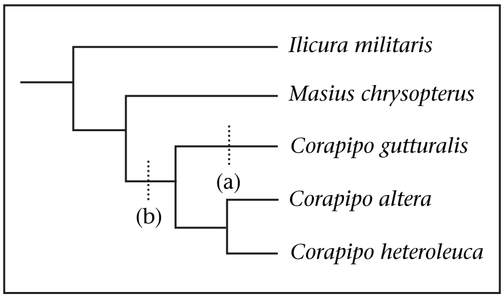

Figure 4. A phylogeny of the *Ilicura–Masius–Corapipo* clade congruent with syringeal, behavioural, and plumage data sets (Prum & Johnson 1987; Prum 1990, 1992, 1997). A male behavioural preference for displaying in noncloudy ambient light conditions (a) evolved as a unique, derived, autapomorphy of *Corapipo gutturalis*. This behavioural change is coincident with a significant increase in the availability of noncloudy conditions in this lineage (a) as predicted by sensory drive, but is not phylogenetically coincident with the origin of the highly contrasting, blue-black and white plumage pattern in the ancestor of all *Corapipo* species (b).

diversification of secondary sexual characters will require not merely examining the correlation between signals and environments, but also whether phylogenetic patterns in signal phenotype evolution match variation in the sensory environment (Prum 1997; Endler & Basolo 1998).

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