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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