**LETTER**

**Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community**

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**Abstract**
Rainforests offer two contrasted light environments: a bright canopy rich in blue and UV and a dark understory, rich in green and orange. Therefore, natural selection for crypsis should favour dark brown signals in understory and bright green signals in canopy, whereas sexual selection for conspicuousness should favour bright yellow-red signals in understory and dark blue and UV signals in canopy. Using spectrometry and comparative analyses, we examined the relationship between ambient light and colour signals in a bird community of French Guiana. It appears that brightness and hue are mostly naturally selected, while UV content of plumage is more likely sexually selected. At each height, both sexes present similar coloration but males display more conspicuous sexually selected patterns than females. These results show that ambient light drives the evolution of colour signals at community scale, and should be considered when studying signalling in other communities and light-contrasted ecosystems.

**Keywords**
ambient light, bird community, colour signal, comparative method, evolutionary strategy, habitat selection, sensory drive, spectrometry, tropical rainforest.


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**INTRODUCTION**

Animal coloration is thought to evolve as a compromise between two antagonistic selection pressures (Endler 1978; Endler 1991): sexual selection that leads signals towards maximal conspicuousness (Andersson 1994) and natural selection, through communication with prey (Rohwer & Paulson 1987) or predators (Cott 1946; Baker & Parker 1979), that selects for maximal crypsis.

The conspicuousness of a visual signal depends on the spectra of the ambient light, the signal and its background. Maximal conspicuousness is achieved for colours which are rich in the wavelengths present in the ambient light and poorly reflected by the background (Endler 1990). In tropical rainforests, ambient light is a highly variable parameter, both in intensity (Bazzaz & Pickett 1980; Chazdon & Fetcher 1984) and spectral composition (Endler 1993; Théry 2001). The canopy receives much more light (review in Bazzaz & Pickett 1980) and shows a higher spatial light diversity than the understory (Endler 1993). Canopy light environment consists of a green background poor in UV and a light composed of large green patches poor in UV and small yellow-orange patches (Endler 1993). With such contrasted light environments, tropical rainforests provide an ideal ecosystem for estimating the relative importance of natural and sexual selection on colour signal evolution.

As birds have well-developed colour vision – sensitivity to UV, potential tetrachromacy (Chen & Goldsmith 1986; Hart 2001) – they offer a good example to question the role of ambient light on colour signals. If visual communication is optimized, colour differences should exist among bird species according to their preferred light habitat and its background (Endler & Théry 1996). Thus, based on the knowledge of ambient light characteristics and background reflectance, we can specifically predict which colour signals will maximize crypsis or conspicuousness (Endler 1993). Signalling for crypsis should lead canopy birds to be brighter (lighter) than ground birds. Crypsis should also select for colours poorly reflecting UV, for green birds in canopy and brown birds in understory. Signalling for conspicuousness should favour brighter orange signals in the understory and darker blue signals in canopy. Further, because there is more contrast between light and vegetation in the canopy for UV
wavelengths, the use of UV signals for conspicuousness may be more prevalent in canopy-dwelling species. We tested these predictions using spectrometry and comparative analyses, separating heights, colour components, sex and selective pressures. Such methods expand considerably upon previous analyses which ignored the visual specificity of birds, confound colour components because of subjective colour scoring (Walther et al. 1999), or did not investigate different heights within the forest (McNaught & Owens 2002). Our methodology can be applied to other communities (amphibians, plants, insects) living in tropical forests or in other light-contrasted ecosystems.

**MATERIAL AND METHODS**

**Species selection**

We selected 40 species (distributed over 22 families and 12 orders; Fig. 1) from a list of 228 species living in the primary rainforest of Nouragues (French Guiana, 4°03′N, 52°42′W). These species had a known phylogenetic position and well-preserved specimens, males and females, from the region of Guiana were available in the collections of the Museum National d’Histoire Naturelle (Paris). Within a species, we measured two to five adults of each sex. Each body was divided into six regions (crown, back, tail, breast, belly and wing) and colour present in each region was recorded by one reflectance spectrum. In addition, any patch identified as distinct in coloration from the six spectra previously measured was recorded by one reflectance spectrum, independently of its location on the bird. For each species, we defined its foraging height (ground G or canopy C) on the basis of visual observation and classification of Thiollay et al. (2001).

**Colour measurements and spectral data analysis**

We performed reflectance measurements with a S-1000 portable spectrometer and a DH-2000 deuterium-halogen light source as in Gomez & Voisin (2002). We extracted colour parameters brightness, chroma and hue from the reflectance spectra (Fig. 2) following the method described by Endler (1990). We also calculated proportional UV reflectance (reflectance in the UV range 300–400 nm divided by total reflectance). For all individuals of each species and sex, we computed mean values of colour

![Figure 1](https://example.com/figure1.png)  
**Figure 1** Phylogenetic tree based on Sibley & Ahlquist’s (1990) phylogeny used in our analyses. The foraging height, canopy (C) or ground (G) is indicated on the left of the names of the 40 species. Species belong to 22 families and 12 orders.
parameters, and calculated an index of colour variation in patterns by computing the standard deviation of each colorimetric variable over all the colour patches of one specimen, and then by averaging this value over all the individuals of the same species and sex.

Comparative analyses

As species share common ancestry, we could not use classic statistics. Hansen’s (1997) adaptation model was the comparative method best suited for our data set. It estimates the importance of an environmental binary factor (in our case, the ambient light) in the determination of one continuous phenotypic trait over phylogenetic time. The model estimates the rate of evolution of each colour component under the environmental pressure, the average value expected in canopy and corrected for phylogeny, and the difference expected between canopy and understory average values corrected for phylogeny, (Table 1). We reconstructed the ancestral states of the environmental factor (light habitat) using MacClade. Using Sibley & Ahlquist’s (1990) phylogeny and assuming that genera were monophyletic, we obtained a 40-species tree with known topology and branch lengths (Fig. 1). As intratip variation should be negligible compared with intertip variation, we separated males and females in analyses because dimorphism could bias our results. We performed our analyses with Compare v 4.4 (Martins 2001) and set the total depth of the trees to 10 to facilitate comparisons with other studies.

RESULTS

Foraging height in forest explained a larger proportion of the colour variation observed in males than in females (Table 1). In canopy, males were brighter, had more UV and more blue and green colours (higher hue angle) than females. Brightness, chroma, hue and proportional UV reflectance were more varied in male than in female patterns (Table 1). For each variable, the difference expected between canopy and understory was greater in males than in females (higher for males in Table 1, Fig. 2).

Canopy males were significantly brighter than ground males ( in Table 1) but females had similar brightness at both forest heights (underlined value in Table 1). In males, brightness evolved slowly in response to a change in forest height, i.e. light conditions.

For both sexes, canopy birds reflected significantly more UV than ground birds ( in Table 1; Fig. 2b). UV reflectance of plumage changed more rapidly with height in females than in males. Canopy birds showed higher mean hue angles and more varied hues in their patterns than ground birds (Fig. 2c; in Table 1). Hue evolved more rapidly than other colour components in response to environmental change. Canopy and ground birds did not differ in their mean chroma or in chroma variation within
DISCUSSION

Natural selection for crypsis

In agreement with the predictions of the natural selection for crypsis, (1) canopy species have developed brighter coloration than understory species. As they follow the vertical gradient in light intensity presented by background and ambient light, they are very likely cryptic at their respective height. (2) Understorey birds display colours mixing red and yellow hues with low brightness, i.e. colours like brown or reddish-brown, whereas canopy-dwelling birds more frequently have green colours. Both colour types would appear cryptic on their respective background, green in canopy and brown in understory.

Canopy birds have more varied colour patterns than ground birds. Forest canopy is a small-mesh mosaic of light habitats (large gaps with whitish light and woodland shade rich in blue wavelengths) whereas the understory is a large-mesh mosaic of light habitats (forest shade rich in green, small gaps rich in yellow-red) (Endler 1993). Consequently, light is spatially more diverse in canopy compared with ground. Increasing colour diversity in patterns may thus result in increasing crypsis by matching the mesh of colour patches of the background.

Sexual selection for conspicuousness

Across species

Variation of hue between species and within coloration patterns is greater in canopy than in understory. This is perhaps because canopy light offers a broader range of wavelengths than understory light for the production of conspicuous and chromatic visual signals. Conversely, the limited range of wavelengths in the understory may have favoured achromatic signals. For example, Marchetti (1993) found a negative correlation between ambient light intensity and the abundance of achromatic stripes in the coloration of Indian warblers. We could not test this relationship with our methodology.

Canopy birds display more UV than understory birds. The greater expression in canopy of conspicuous signals may originate from (1) a less intense selection for crypsis in canopy or (2) a greater efficiency of UV signals for conspicuousness in canopy. The latter hypothesis is sup-

Table 1  Relationship between colour and foraging height for 40 mature primary rainforest bird species: phylogenetic analysis with Hansen’s adaptation model. Phylogenetic analyses were performed on a 40-species tree, of a total depth set to 10 units of time. $R^2$ (×100) describes the overall fit of the model. The rate of evolution of a colour in response to a change in the environmental factor reflects the intensity of the light as selective factor. The rate of evolution is considered as low when between 0 and 3, moderate between 3 and 7, high when exceeding 7. $O_C$ is the colour phenotype (average value weighed for phylogeny) expected under canopy ambient light and $O_{C-G}$ is the difference between colour phenotypes (between average values weighed for phylogeny) expected between canopy and ground light environments. Standard deviations (SD) are on the right of the phenotypes values. Italicized values of $O_{C-G}$ are those for which standard deviations are equal or higher than the difference value. Note that in these cases, difference between canopy and ground values can be positive or negative and is no longer significant.

<table>
<thead>
<tr>
<th>Sex Colour variable</th>
<th>$R^2$</th>
<th>Rate of evolution</th>
<th>$O_C$</th>
<th>sd</th>
<th>$O_{C-G}$</th>
<th>sd</th>
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<td></td>
<td></td>
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<tr>
<td>Hue</td>
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<td>5.52</td>
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<td>40.36</td>
<td>6.81</td>
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<td>0.18</td>
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<td>0.02</td>
<td>0.06</td>
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<td>Chroma diversity</td>
<td>1.3</td>
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<td>0.02</td>
<td>0.03</td>
<td>0.07</td>
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<tr>
<td>Hue</td>
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<td>84.14</td>
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<td>Chroma diversity</td>
<td>2.81</td>
<td>0.3</td>
<td>0.12</td>
<td>0.02</td>
<td>0.06</td>
<td>0.06</td>
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</table>
ported by data on ambient light characteristics: the poverty of understory light in UV may impose a limit to conspicuousness of UV signals in the understory (Fleishman et al. 1993). However, this is not supported by the higher rate of evolution of UV reflectance in female plumages.

Absence of differences in chroma between species and heights does not imply that chroma may not be selected. Within species, variations in chroma between individuals may offer a substrate for sexual selection.

Within species
Males are brighter, have more colours rich in short wavelengths than females in canopy, while in understory males are darker and have more orange and red colours than females. A greater range of hues in their patterns testifies that males display more varied colours than females. Because of their distinct roles in reproduction, female birds are thought to be more selected for crypsis while males are often selected to display conspicuous colours (Wallace 1889; Baker & Parker 1979; Endler 1991). Given female coloration as reference for maximal crypsis, males diverge from this cryptic pattern and appear more conspicuous. This is consistent with intra- or interspecific studies showing that, through sexual selection, males use different colour signals and light habitats at each display height to maximize visual contrast against the background and/or within their coloration pattern (Endler & Théry 1996; Heindl & Winkler 2003a; Heindl & Winkler 2003b).

Our results suggest that general patterns of plumage coloration in tropical forest birds were mainly governed by natural selection for crypsis. Using colour scoring based on human vision, Walther et al. (1999) could only conclude that canopy birds were more colourful than ground birds. Without separating heights in the forest, McNaught & Owens (2002) found that forest birds were darker than birds from open habitats. Our methodology (spectrometry and comparative analyses, separating heights, colour components, sex, and selective pressures) revealed variations that had not been detected by previous studies, especially sex-dependent differences and the importance of UV in bird coloration.

In terms of both mean coloration and colour diversity, ambient light appears to constrain more hue and proportional UV reflectance than brightness or chroma. However, in all our analyses, ambient light explains only a small part of the variations observed. Other factors like mating system or position of species in the food web can account for the rest of colour variations. Nevertheless, ambient light likely plays a major role, either as a proximate factor (sensory drive hypothesis of Endler 1992) or an ultimate factor (exploitation of receiver-biased preferences; Ryan 1990) in controlling coloration evolution. This study highlights the importance of considering ambient light when investigating the evolution of colour signals, not only in birds but also in other communities (plants, insects, amphibians) and/or light-contrasted ecosystems.

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