

Dusk light environment optimizes visual perception of conspecifics in a crepuscular horned beetle

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Variation of visual signal coloration has been predicted among closely related species or populations by the sensory drive hypothesis and tested in fishes, reptiles, or birds. However, despite the tremendous diversity of insect colorations and habitat preferences, sensory drive constrained by habitat transmission through different light environments has not been investigated in this group. Here, we study in a strictly crepuscular horned beetle (*Coprophanaeus lancifer*) the relationship between body coloration, ambient light spectra, and conspicuousness to conspecifics. We estimate brightness contrast of the mean coloration, as it is seen at relatively long distance, and color contrast of the horn seen in front of the pronotum, as it is seen during interindividual contests occurring at short distance, using a physiological model of crepuscular horned beetle vision. As predicted, brightness contrast of the mean coloration is optimal in the dusk ambient light spectrum compared with diurnal light environments. Similarly, color contrast of the horn seen in front of the pronotum is maximal in dusk light compared with other forest light environments. Dusk light favors both chromatic and achromatic detection of *C. lancifer* by conspecifics, which is critical for pair formation during this restricted time window. We created varying reflectance spectra and calculated their conspicuousness under different light environments: maximal color contrast is obtained for the combination beetle signal–dusk light environment. This quantitative example of adaptation of body coloration to ambient light spectrum is the first insight into sensory drive through habitat-mediated transmission of a color signal in an insect species. **Key words:** ambient light, physiological model, sensory drive, visual contrast. [*Behav Ecol* 19:627–634 (2008)]

The sensory drive hypothesis explains the evolution of communication signals by integrating sensory systems and communication behaviors under the constraints of physical characteristics of the signaling environment and neurobiology of perception (Endler 1992). According to this hypothesis, particular signals of the sender are favored if they are easy to detect by the receiver. In this context, signal evolution is potentially influenced by the process of habitat transmission, which results from the interaction between physical characteristics of the local environment and signal design.

Structural heterogeneity, typical of complex ecosystems such as forests or coral reefs, creates distinct light environments differing in ambient light quality, intensity, directionality, and visual background (Endler 1993; Marshall 2000). For example, forest shade, woodland shade, small gap, and large gap are contrasted light habitats coexisting in tropical forests under clear weather (Endler 1993). In addition, the early/late light environment is generated by increased filtering of sunlight through the atmospheric ozone layer at low sun angles and is present everywhere in the forest at dawn and dusk. As a consequence, visual signals used for either crypsis or conspicuousness are often precisely adapted to distinctly different light environments or backgrounds between closely related populations or species, as it has been shown in fishes (e.g., Reimchen 1989; Endler 1991; Seehausen et al. 1997; Marshall 2000; Fuller 2002; Maan et al. 2006), birds (Marchetti 1993; Endler and Théry 1996; McNaught and Owens 2002;

Gomez and Théry 2004, 2007), or lizards (e.g., Leal and Fleishman 2002, 2004). Surprisingly, if sensory drive through light environments has been demonstrated in such a wide array of animal species, this hypothesis has not been investigated in insects, even though they display extremely diverse colors. To our knowledge, only 1 study intended to determine the conspicuousness of insect color patterns within their respective light environments by using reflectance spectrometry and ambient light irradiance (Schultz 2001). However, this study did not take into account visual sensitivities, only compared contrast of the larger color patch with the background between large gaps and forest shade, and its results were not interpreted in terms of sensory drive. Butterfly wing color patterns have been contrasted with flying height in neotropical rain forests (Papageorgis 1975; Burd 1994; Mallet and Gilbert 1995), but none of these studies measured animal, background, or ambient light color, which are all necessary to determine how the physical environment does impact the efficiency of a signal.

Because it is difficult to follow the flight of an insect and precisely determine in which light habitat its activities are performed, we decided to investigate the relationship between body coloration and ambient light spectra in a crepuscular species, by consequence only active in the early/late light environment. We choose to study the scarab horned beetle *Coprophanaeus lancifer* a deep violet–blue species active above ground only at dusk (Feer and Pincebourde 2005; see also Results). *Coprophanaeus lancifer* and its close relative, *Coprophanaeus ensifer*, are the largest phanaeine species and among the largest known Scarabeinae, reaching a body length of 56 mm (Edmonds 1972; Arnaud 2002). *Coprophanaeus lancifer* is widely distributed in tropical rain forests of the Amazon Basin. Together with *Coprophanaeus bonariensis* and *C. ensifer*,

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C. lancifer is characterized by its reduced sexual dimorphism compared with other species of the genus and phanaeines in general, both sexes having a greatly developed horn which is always greater in males, although this difference is less obvious in small or moderately developed individuals (Otronen 1988; Arnaud 2002).

Recent evolutionary ecology research on horn and dung beetles has been particularly focused on the evolution and functions of the horn (e.g., Otronen 1988; Emlen 1996; Lailvaux et al. 2005; Moczek et al. 2006; Pomfret and Knell 2006; Simmons and Emlen 2006; and references therein). Despite their diverse and often spectacular coloration, few studies have investigated the nature or function of color in horned beetles: Vulinek (1997) published a review on characteristics and function of iridescence and provided qualitative results on ultraviolet (UV) reflectance and Watanabe et al. (2002) conducted a quantitative analysis of geographic color variation in 2 Japanese species showing convergent evolution of color within each study sites. Different hypotheses, including aposematism and social signaling, have been evoked to explain the often bright coloration of horned beetles (review in Vulinek 1997), but no study has ever considered the possibility that ambient light spectra can drive the evolution of the coloration in these insects.

Here we investigate if visual contrasts generated by the horned beetle seen by conspecifics against the visual background are more pronounced in the crepuscular ambient light than in diurnal light environments. Brightness contrast is known in both birds and insects to be used for target detection at long distance and color contrast for detection at short distance (Osorio, Miklósi, and Gonda 1999; Osorio, Vorobyev, and Jones 1999; Spaethe et al. 2001). Over distance colors of a pattern combine because of blurring resulting from poor resolution. Consequently, we quantified brightness contrast using mean body coloration to evaluate conspicuousness at long distance. In contrast, at short distance, visual acuity allows separation of different elements of a color pattern. At short distance, both intra- and intersexual fights have been observed in the studied species (Larsen T, personal communication) and in the closely related species *C. ensifer* (Otronen 1988), with individuals facing off against each other. These contests are most probably visually mediated. Because of the eye location (Figure 1b), fighting individuals cannot see the whole body of their opponent. More likely, they use the visual contrast of the dark horn against the bright pronotal shield to locate each other (Vulinek 1997). Therefore, we used the horn/pronotum visual contrast to evaluate conspicuousness at short distance. Our predictions for the optimization of visual communication at dusk compared with diurnal light habitats are that 1) brightness contrast should be maximal at long distance and 2) color contrast should be maximal at short distance.

MATERIALS AND METHODS

Study site

The study was conducted in undisturbed primary tropical rain forest at the Nouragues Centre National de la Recherche Scientifique Biological Station in French Guyana (4°03'N, 52°42'W; Bongers et al. 2001).

Temporal pattern of activity

In order to determine the daily flight activity of *C. lancifer*, we used 11 pitfall traps made from plastic containers (11.5 cm in height and 11 cm in diameter) placed at ground level and spaced every 20 m along a linear transect of 200 m. The bait

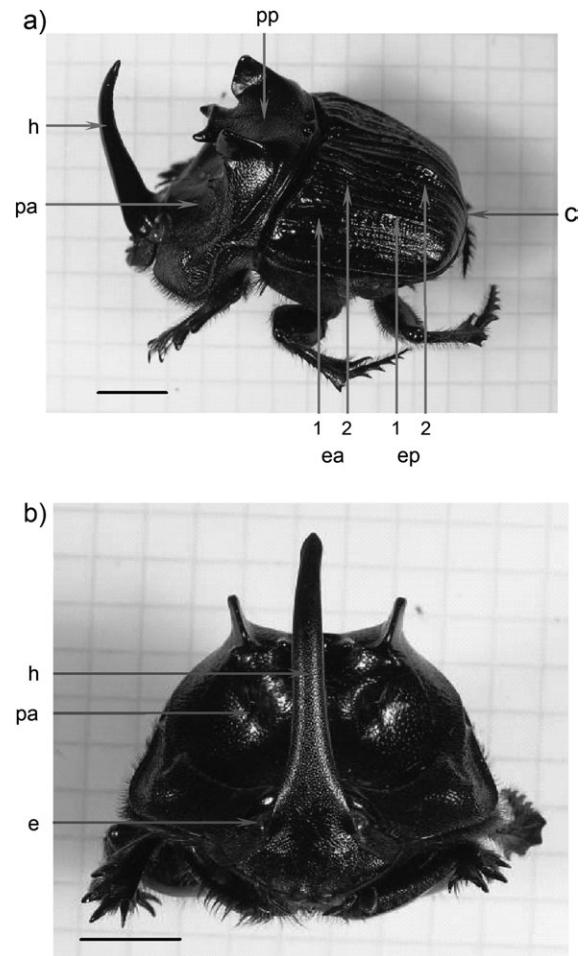


Figure 1
(a) Lateral view of *Coprophanaeus lancifer* with the locations of reflectance measurements. h, horn; pa, pronotum anterior; pp, pronotum posterior; ea 1 and 2, elytron anterior; ep 1 and 2, elytron posterior; c, caudal part. (b) Frontal view of *C. lancifer*: h, horn; pa, pronotum anterior; e, eye (not measured). Scale bar = 1 cm.

(meat left outside for a day, human dung) was left in a small wire netting madding box and suspended inside the trap (as in Feer and Pincebourde 2005). Insects were collected each hour at dawn and dusk (respectively at 0500, 0600, and 0700 h and dawn occurring around 0600 h and at 1700, 1800, and 1900 h and dusk occurring around 1800 h) and every 2 h during nocturnal and diurnal periods. Individuals were identified and counted. This protocol was conducted in April, May, and October 2001 and in April 2002 with a total of 210 trap days. Direct observations of flying individuals were also conducted throughout the Nouragues Reserve, and flying times were compared with results of trapping.

Spectral measurements

Measured insects (14 females and 8 males) collected at Nouragues between 1995 and 2002 are deposited in the Muséum National d'Histoire Naturelle (Brunoy) collection. Reflectance spectra were measured at 8 locations on each individual: the horn (frontal side), the pronotal surface (anterior lateral side and posterior median side), the elytron (2 anterior locations and 2 posterior locations), and the caudal part (Figure 1). Individuals were dissected after all measurements to determine their sex.

Reflectance spectra (beetles coloration and litter visual background) were measured using an Ocean Optics S2000 spectrometer calibrated between 200 and 850 nm and a deuterium–halogen light source DH-2000 emitting between 215 and 1700 nm, relative to a 99% (300–700 nm) reflectance standard (Spectralon™) and to the dark current. The dark noise and the white reference were taken before measuring each beetle or visual background, and wavelength calibration was checked with a Mercury–Argon light source (HG1 Ocean Optics) before and after the experiment. Because of the small horn width, beetle structural coloration was measured at 90° to normal using a 1.5-mm-diameter sensor FCR-7UV200-1.5x100-2 inserted in a miniature black chamber at 1 mm from the cuticle, as in Théry et al. (2005).

We used forest litter as visual background because individuals meet and interact on the forest floor to mate or to compete for food (Feer F, Pincebourde S, Théry M, personal observation; Larsen T, personal communication; Otronen 1988 in *C. ensifer*). Reflectance spectra of the litter were measured at 45° (to avoid specular reflectance) with the same spectrometer and light source and with a 2 × 3-mm area sensor FCR-7UV200-2-45 through a silica window that guaranteed a constant measuring distance. Mean litter spectrum was computed by averaging 70 reflectance spectra of leaf litter randomly sampled along the insect-trapping transect.

We measured ambient light along the insect-trapping transect with the same spectrometer using a CC3-UV cosine-corrected irradiance sensor connected to a FC-UV600-2-ME fiber optic and calibrated in micromoles per square centimeter seconds with an Avantes AvaLight-DH-CAL deuterium–halogen light source. The irradiance sensor was placed vertically at ground level, and spectra were recorded between 8 and 16 February 2001 and 10 and 23 October 2001 from 0530 to 1900 h at the rate of 1 spectrum per min in the dawn and dusk periods and 1 spectrum per 5 min in the daylight period. An average irradiance spectrum was calculated for the forest shade, woodland shade, large gap, and small gap light environments (Endler 1993) from 100 habitat-representative spectra. Light measurements were conducted during 2 dry seasons with low cloud cover. Because the spectra of all diurnal light environments converge toward that of large gaps during cloudy weather (Endler 1993), cloudy spectra were removed from the analysis. Of the 19 individuals sampled, 5 were trapped or observed flying between 1740 and 1800 h and 14 between 1800 and 1900 h (see Results). Therefore, to compute the irradiance spectrum representative of the activity of *C. lancifer*, we averaged 25 irradiance spectra measured between 1740 and 1800 h and 70 irradiance spectra measured between 1800 and 1900 h.

Color and brightness contrasts

The visual model computes photoreceptor stimulations when the horned beetle is viewing a color patch against the visual background in a defined light environment. Because characteristics of the *C. lancifer*'s visual system or of others phanaeines are unknown, we used photoreceptor types and spectral sensitivities of *Onitis alexis* (Coleoptera, Scarabaeidae, Onitini). Both Onitini and Phanaeini belong to the same subfamily (Coprinae; Cambefort 1991). As *C. lancifer*, *O. alexis* is crepuscular and shows peak flight activity at dusk (Houston and McIntyre 1985). This species has 2 types of photoreceptors, the UV type with maximal sensitivity at 370 nm and the G type with maximal sensitivity at 540 nm and a small secondary peak in the UV wavelengths (Warrant and McIntyre 1990; see Figure 2a). The sensitivity of this species to polarized light is very low and is unlikely to play a major role in the beetle's visual behavior (Warrant and McIntyre 1990). The eye design

of most Scarabaeidae makes possible the discrimination of colors (Horridge 1975).

We used a model of visual discrimination, which computes the color distance ΔS between the beetle and its visual background as follows:

$$\Delta S^2 = \frac{(\Delta f_1 - \Delta f_2)^2}{(e_1^2 + e_2^2)}, \quad (1)$$

where Δf_i is the log ratio of the quantum catches for cone i for colors A and B.

$$\Delta f_i = \log \frac{Q_{iA}}{Q_{iB}} = \log \frac{\int_{300}^{700} R_A(\lambda) \times I(\lambda) \times S_i(\lambda) d\lambda}{\int_{300}^{700} R_B(\lambda) \times I(\lambda) \times S_i(\lambda) d\lambda}, \quad (2)$$

where $R_A(\lambda)$ is the reflectance spectrum of the color signal A, $R_B(\lambda)$ the reflectance spectrum of the visual background B, $I(\lambda)$ is the irradiance spectrum of the ambient light, and $S_i(\lambda)$ is the cone spectral sensitivity. We considered the noise of cone class i , e_i , to depend only on neural noise (Håstad et al. 2005), with a Weber fraction ω of 0.05, and η_i describing the relative density of cone class i in the retina.

$$e_i = \frac{\omega}{\sqrt{\eta_i}}. \quad (3)$$

After Warrant and McIntyre (1990), we considered that the relative density of UV and G types of cones was 1:4.

Luminance detection was computed from G photoreceptors' excitation signals, as for honeybees which are known to use this receptor type to perceive brightness contrast at long range or to detect small targets (Spaethe et al. 2001). For the brightness contrast ΔS_Q between the color A and the background B, we proceeded as Siddiqi et al. (2004):

$$\Delta S_Q = \frac{|\Delta f_Q|}{e} = \frac{\left| \log \frac{Q_{QA}}{Q_{QB}} \right|}{e} = \frac{\left| \log \frac{\int_{300}^{700} R_A(\lambda) \times I(\lambda) \times S_Q(\lambda) d\lambda}{\int_{300}^{700} R_B(\lambda) \times I(\lambda) \times S_Q(\lambda) d\lambda} \right|}{e}. \quad (4)$$

where $S_Q(\lambda)$ is the spectral sensitivity function of the G cones, and e describes the neural noise associated with these cones (see Equation 3).

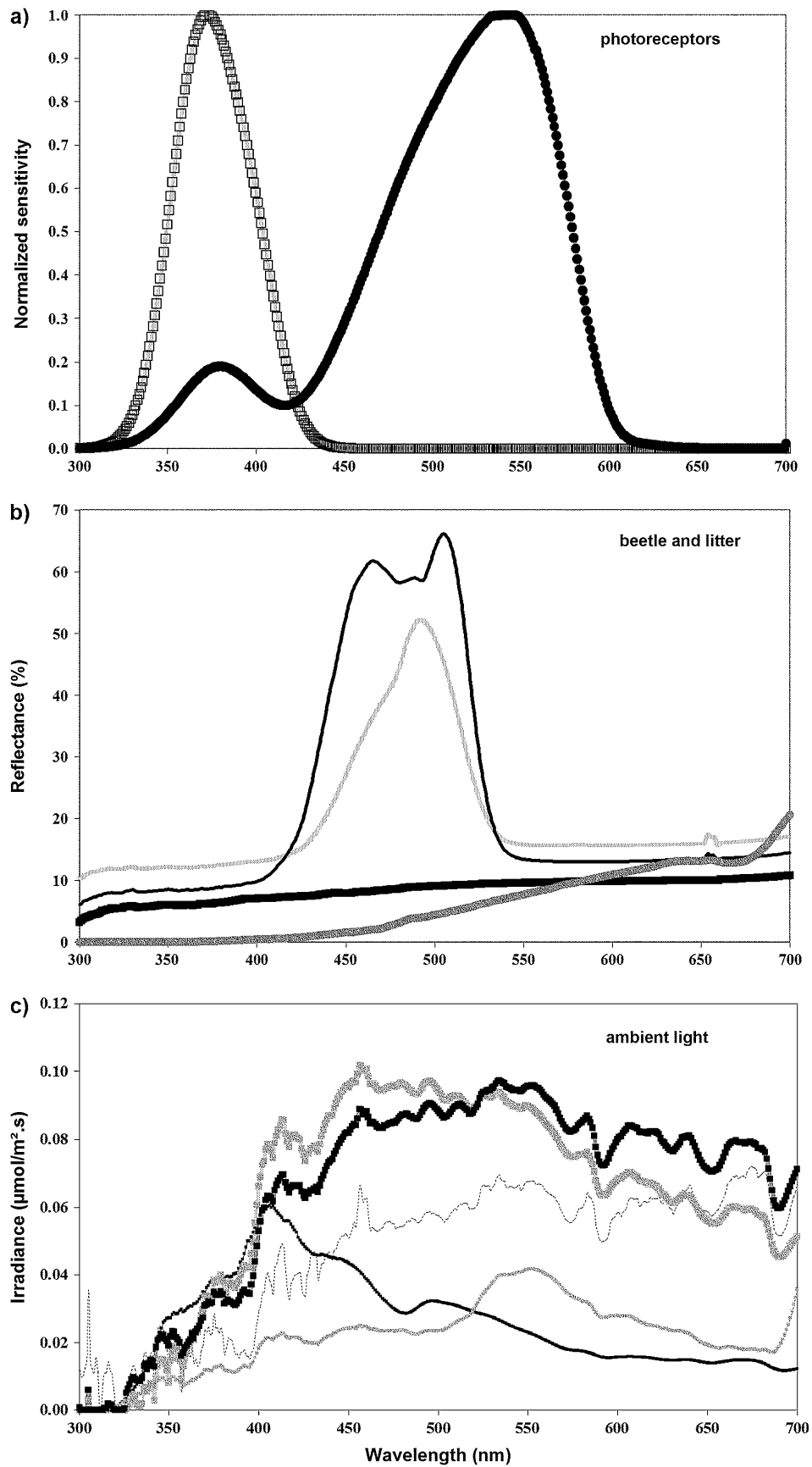
At long distance, visual acuity does not allow separating each individual body part from the visual background, and brightness contrast is used for visual discrimination (Spaethe et al. 2001). Therefore, we computed brightness contrast of the average body coloration against the litter background. At short distance, individuals face each other during interindividual challenges (Otronen 1988), and color contrast is used for visual discrimination (Spaethe et al. 2001). In this posture, the horn is viewed against the pronotum due to the beetle morphology. We thus computed color contrast CC per individual i by calculating the coefficient of variation between contrasts of the horn and pronotum against the background:

$$CC_i = \frac{\text{standard deviation}(\Delta S_{\text{horn}_i}; \Delta S_{\text{pronotum}_i})}{\text{mean}(\Delta S_{\text{horn}_i}; \Delta S_{\text{pronotum}_i})}. \quad (5)$$

We used the coefficient of variation because the greater the variation among patches relative to the mean the stronger the color contrast between patches (Endler 1990).

The effect of shifting reflectance spectra

To investigate the optimality of *C. lancifer* coloration for visual detection in the crepuscular light environment, we shifted



reflectance spectra of each individual (mean reflectance spectrum and horn and pronotum reflectance spectra) along the wavelength axis and computed brightness and color contrasts of shifted spectra, which we statistically compared with visual contrasts of the nonshifted spectra. Spectral shifts were conducted every 20, 40, and 60 nm toward both shorter and longer wavelengths.

Statistical analysis

To test for sexual differences in brightness and color contrasts among the 22 individuals, we used 1 Mann–Whitney U -test for each of the 5 light environments.

To test whether individual brightness and color contrasts differed between light environments, we used 10 paired t -test corresponding to each of the possible combinations of light environments, with Bonferroni adjustment for multiple tests.

To test whether individual brightness and color contrasts differed when spectra were shifted every 20, 40, and 60 nm toward both shorter and longer wavelengths, we used 22 paired t -test corresponding to each of the possible combinations between resulting spectra, with Bonferroni adjustment for multiple tests.

All analyses were performed using SYSTAT 9.01. Significance was set at the 0.05 level, and results are reported as mean \pm 1 standard deviation.

RESULTS

Beetle and litter coloration

The mean beetle coloration is blue-green with a sharp peak of reflectance reaching 52% at 495 nm (Figure 2b). The reflectance spectrum of the pronotum shows the same hue and is the only measured location with 2 peaks of reflectance at 465 and 505 nm. The pronotum is the brightest body location, peaking at 65% of reflectance. The horn is black, with a nearly flat spectrum below 10% reflectance. The litter visual background is dark brown. There is no peak in UV reflectance either on the beetle or on the visual background.

Irradiance of the light environments

At dusk, ambient light is UV blue with dominant wavelengths between 345 and 480 nm peaking at 405 nm (Figure 2c). Forest shade is greenish with a peak at 550 nm. Woodland shade is bluish with an irradiance spectrum peaking at 455 nm. Small gaps are yellow-orange, dominated by long wavelengths. Large gaps are whitish with a flatter spectrum in the visible wavelengths. Mean light intensity is very low at dusk ($1.0 \mu\text{mol}/\text{m}^2 \text{ s}$ between 300 and 700 nm), compared with forest shade ($8.6 \mu\text{mol}/\text{m}^2 \text{ s}$), woodland shade ($25.0 \mu\text{mol}/\text{m}^2 \text{ s}$), small gaps ($188.8 \mu\text{mol}/\text{m}^2 \text{ s}$), and large gaps ($1302.9 \mu\text{mol}/\text{m}^2 \text{ s}$).

Temporal pattern of activity

Among the 9 trapped individuals, 8 were captured between 1800 and 1900 h at the end of the dusk period (Figure 3). Only 1 individual was trapped between 1700 and 1800 h, and *C. lancifer* was never observed or caught during another period of the day (Figure 3) or in the nocturnal period. Moreover, 10 individuals were observed flying through the forest:

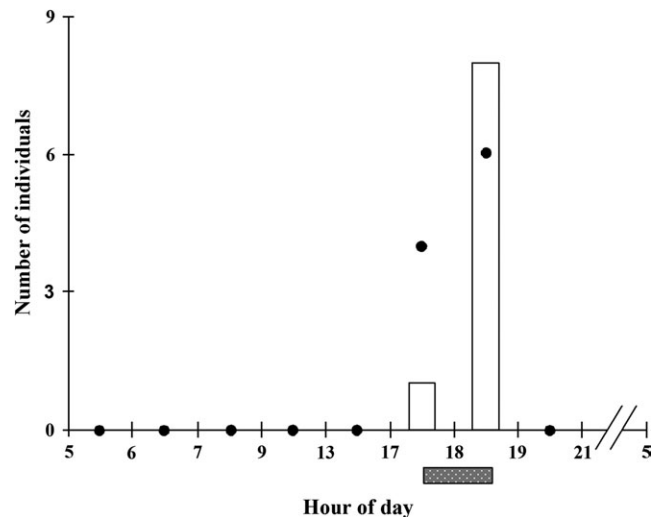


Figure 3

Daily flight activity of *Coprophanaeus lancifer* determined using both a specific trapping method (number of captured individuals, bars) and visual observation of individuals flying through the forest (number of observations, dots). The x axis represents each hour interval of trapping method. The nocturnal part is not represented (beetle has been neither trapped nor seen in flight during the night). The hatched gray bar shows the dusk period.

between 1700 and 1800 h and 6 between 1800 and 1900 h (Figure 3). The earliest observation was made at 1740 h. Therefore, *C. lancifer* appears to be strictly crepuscular and to fly only at dusk.

Visual contrasts of the beetle mean coloration

There is no sexual difference in brightness contrast in either of the light environments ($n = 22$ individuals, $n = 5$ matched pairs tests, all Mann–Whitney $U > 43$, $P > 0.37$).

Brightness contrast is significantly higher in the dusk light environment than in any daylight environment (Figure 4; $n = 10$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals, all $t > 63.9$, all $P < 0.001$). Using brightness contrast at long distance, the mean beetle coloration is more contrasting against the litter background in the dusk light environment than in woodland shade, large gaps, small gaps, or forest shade.

Shifting the mean coloration toward shorter wavelengths strongly reduces brightness contrast in dusk ambient light (mean difference -6% for 20 nm, -13% for 40 nm, -18% for 60 nm; $n = 11$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals, all $t < -35.2$, all $P < 0.001$). Shifting spectra toward higher wavelengths slightly increases brightness contrast for both 20- and 40-nm shifts (mean difference $+4\%$ for both shifts; $n = 11$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals; $t = 19.23$, $P < 0.001$ for 20 nm; $t = 8.4$, $P < 0.001$ for 40 nm), but not for a 60-nm shift (paired t -test with Bonferroni adjustment for multiple tests, $n = 22$ individuals, $t = -1.27$, $P = 1$).

Figure 2

(a) Normalized sensitivity of *Onitis alexis* photoreceptors (after Warrant and McIntyre 1990). White squares, UV type and black circles, G type. (b) Reflectance spectra of *Coprophanaeus lancifer* and the litter visual background used in the vision model. Thin black line, pronotum; thin gray line, mean coloration; thick black line, horn; thick gray line, litter. (c) Irradiance spectra of the forest light environments; to allow comparison the intensity of dusk irradiance has been multiplied by 10, that of large gaps divided by 10, and that of small gaps divided by 10. Thick gray line, woodland shade; thick black line, large gap; dotted line, small gap; thin black line, dusk; thin gray line, forest shade.

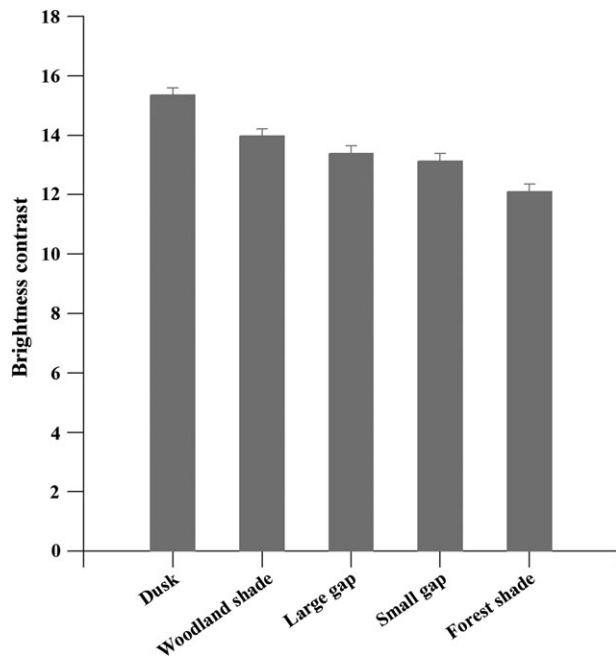


Figure 4
Brightness contrasts (mean \pm standard deviation) of the mean beetle coloration against the visual background in the different light environments ($n = 22$ individuals).

Visual contrasts of the horn in front of the pronotum

There is no sexual difference in color contrast in either of the light environments ($n = 22$ individuals, $n = 5$ Mann–Whitney tests, all $U > 64$, $P > 0.49$).

Color contrast of the horn seen in front of the pronotum is significantly higher in the dusk light environment than in any daylight environment, except for woodland shade which generates equivalent contrast (Figure 5; $n = 10$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals; $t = 2.5$, $P < 0.05$ between dusk and woodland shade; $t > 11.4$, $P < 0.001$ between all other combinations of light environments). Using color contrast at short distance, the horn/pronotum color contrast is more visible in the dusk light environment than in large gaps, small gaps, or forest shade.

Shifting horn and pronotum spectra toward shorter wavelengths strongly reduces color contrast in dusk ambient light (mean difference -42% for 20 nm, -74% for 40 nm, -52% for 60 nm; $n = 11$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals, all $t < -5.4$, all $P < 0.001$). However, shifting spectra toward higher wavelengths is neither increasing nor decreasing color contrast ($n = 11$ paired t -tests with Bonferroni adjustment for multiple tests, $n = 22$ individuals, all $t > -2.5$, all $P > 0.43$).

DISCUSSION

Our results show that body coloration of *C. lancifer*, as seen through the crepuscular horned beetle visual system, contrasts more against the visual background in the dusk light environment than in any diurnal light environment measured in tropical rainforest understory. Shifting reflectance spectra toward shorter wavelengths reduces both brightness contrast of the mean coloration and color contrast of the horn seen in front of the pronotum. However, shifting reflectance spectra toward longer wavelengths increases brightness contrast of the mean coloration up to 40 nm, but not horn–pronotum

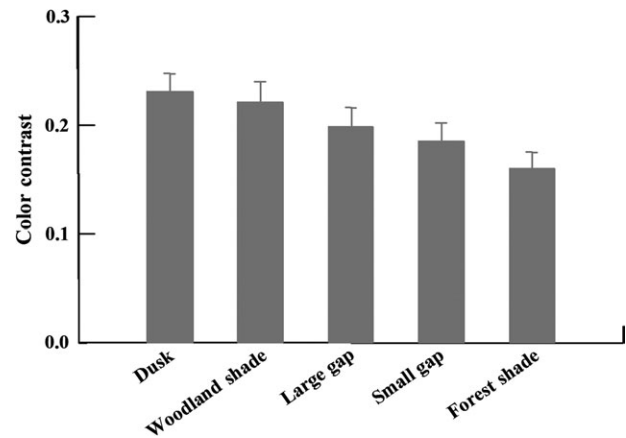


Figure 5
Color contrasts (mean \pm standard deviation) of the horn seen against the pronotum in the different light environments ($n = 22$ individuals).

color contrast. Therefore, the spectral locations of reflectance spectra appear as optimal for visual detection at short distance in forest understory at dusk. *Coprophanaeus lancifer* is active above ground only around dusk, when the appearance of its body coloration to conspecifics is optimized at short distance in the dusk light environment. These results strongly support the hypothesis of sensory drive through habitat transmission of the visual signal in dusk ambient light. It was already known that light intensity plays a major role in determining the onset of flight activity in dung beetles (Houston and McIntyre 1985; Caveney et al. 1995), though the temporal window of activity could also be explained by avoidance of interspecific competition for resource (ecological segregation) or predation pressure (e.g., Hanski and Cambefort 1991). However, to our knowledge, it has never been shown that a specific light spectrum optimizes conspicuousness of body coloration as seen through the visual system of any insect species.

At long distance, brightness contrast is likely used to detect mean body coloration against the background, whereas at short distance, individuals of both sexes face each other and likely use the color contrast of the horn in front of the pronotum for visual detection (Vulinec 1997). Resolution of the eye of the closely related species *O. alexis* allows the beetle to separate different elements of the color pattern if the individual is closer than about half a meter (Warrant and McIntyre 1990). Therefore, we consider that brightness contrast of the mean coloration is used farther than half a meter and that color contrast of horn seen in front of the pronotum is used closer than half a meter. Once horned beetles have located a carcass (probably by olfaction), they look for a sexual partner, build a nesting burrow, then copulate, and provision the burrow with larval food in the form of brood balls each receiving only 1 egg. In the closely related species *C. ensifer*, intra- and intersexual fights using the horn are commonly used both for pair formation and for competition in each others' burrows (Otronen 1988). Rapid detection by achromatic and chromatic cues favored by ambient light at dusk is probably critical for pair formation during this restricted time window.

The tremendous diversity of insect coloration has for long intrigued naturalists and evolutionary ecologists. Several functions have been assigned to insect coloration, including regulation of body temperature (Forsman et al. 2002; Pereboom and Biesmeijer 2003), aposematism and mimicry (e.g., Schultz 2001; Turner 2005; Prudic et al. 2007), success in mate choice

(Breuker and Brakefield 2002; Llopart et al. 2002; Kromforst et al. 2006) or in contest competition (Grether 1996), lifetime indication of juvenile environment (Kemp and Rutowski 2007), and improved immune function or parasite resistance (e.g., Siva-Jothy 2000; Joop et al. 2006). Here, we show how habitat choice may drive the evolution of body coloration patterns to optimize their detection by conspecifics. As for the present study of *C. lancifer*, sensory drive through habitat transmission of visual signals may bring new insights on the interplay between the environmental constraints and the evolution of insect coloration.

Structural coloration in *C. lancifer* seems likely given the rarity of biological blue pigments and the relatively narrow-band reflectance of the body surface. Many other insect species use structural color for mating displays, but why a pigment would not suffice in most of these cases is usually unclear. This study seems to provide a novel example of why elaborate structural color might have evolved rather than a pigment in *C. lancifer*. In this case, structural color appears to optimize a chromatic signal in a very specific crepuscular light environment in a way that a longer wavelength reflective pigment would not.

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