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Elytra Absorb Ultraviolet Radiation but Transmit Infrared Radiation in Neotropical *Canthon* Species (Coleoptera, Scarabaeinae)

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ABSTRACT

Strategies to deal with global radiation may be related to important aspects of species biology and ecology by reflecting, transmitting or absorbing the radiation of varying wavelengths differently. The elytra capacity to manage infrared, visible and ultraviolet radiations (from 185 to 1400 nm) was assessed with a spectrophotometric analysis in five *Canthon* species of dung beetles; we calculated the reflectance, transmittance and absorbance capacity of the elytra of these species. These species have different ecologies: two species preferentially inhabit forest areas (*Canthon angularis* and *Canthon lividus lividus*), two species preferentially inhabit open areas (*Canthon chalybaeus* and *Canthon tetraodon*) including agricultural crops, and one species does not present a clear habitat preference and can be found in both habitats (*Canthon quinquemaculatus*). All the species show a similar pattern in which the light from shorter wavelengths and higher frequencies is almost entirely absorbed by the elytra, while radiation from longer wavelengths and lower frequencies can mostly pass through the elytra. However, *C. quinquemaculatus* seems to have significantly higher rates of reflectance and transmittance in the visible- and near-infrared spectrum. This different pattern found in *C. quinquemaculatus* may be associated with its capacity to establish populations both in agricultural and forest areas.

INTRODUCTION

The sun is the major source of radiation on Earth and plays a crucial role in the evolution of life (1). The sunlight reaching Earth's surface is called global radiation (2) and is frequently classified into three ranges (based on human vision) for biological studies according to their electromagnetic wavelength: infrared, visible and ultraviolet radiation. These radiations may affect all living organisms. Distinct radiations have different energies, and energy increases as the wavelength decreases. Thus, species capacity to deal with each type of radiation—reflecting, absorbing or transmitting it—may affect important aspects of their biology. In insects, transmitting infrared radiation into the body can increase internal body temperature, influencing their development (3), immune system regulation (4), fertility (5), foraging habit (6) and morphology (7). Reflecting infrared radiation can prevent overheating, which helps individuals to maintain optimal temperatures, as high temperatures (mostly over 50°C) are fatal for many insects, as well as for dung beetles (8).

Visible radiation is responsible for the abundant color variation observed in insects and is an important feature interfering in species behavior, ecology and physiology. Coloration patterns may be associated with the quality of the immune system (9), which can influence mate choice and consequently sexual selection (10). Other evolutionary processes may drive coloration patterns; especially, important is the pressure of predation, where individuals develop color patterns for camouflage (11), as a warning (aposematic) (12) or mimicry. In Coleoptera (13), and specifically in dung beetles (14,15), color variations cannot be pigmentary, but structural. Thus, beetle's color is sometimes understood as a pure physical mechanism due to material properties of the exoskeleton which reflects, scatters and deflects the light. Coloration also has a possible role in thermoregulation (16). Experiments with the grasshopper *Kosciuscola tristis* showed that increasing the ambient temperature (from 15°C to 25°C) activates intracellular granule migration that changes insect color from black to blue (17,18). This color change has a thermoregulatory function, as the black coloration is associated with heat absorption at lower temperatures (19). Therefore, coloration presents two distinct aspects: ecological (associated with species interactions) and physiological (related to species homeostasis). These two evolutionary paths suggest the existence of a trade-off between ecological and physiological investment. Furthermore, coloration can be associated with species habits, for example, in tropical dung beetles, black species are usually nocturnal while diurnal species are colorful (20). This pattern was only observed in large species (>1 cm) as small species may be black and diurnal (20). Thus, associated with color, the organism's morphology (*i.e.* weight, volume) is an important aspect that may be related to individual responses to solar radiation.

Ultraviolet radiation causes serious mutagenic deleterious effects on organisms due to the high photon energy, causing mortality (21), development inhibition (22) and affecting species interactions (23,24). As a consequence, many insects are associated with environments with low ultraviolet rates (25). Ultraviolet radiation has a high penetration power, and its transmittance into the body should be a negatively selected strategy, as individuals would suffer internal damages. Therefore, behavioral (26) or physical (27) mechanisms to avoid ultraviolet radiation are frequent in animals.

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The elytra of Coleoptera, which are composed of an exocuticle and endocuticle structured by chitin fibers in a matrix with lipids and proteins, have many functions (28–30). The cuticle can act as barrier against external influences, such as water (31,32), pathogens (33) and radiation (34). In this study, we examine, for the first time, the elytra spectrophotometric response of Neotropical dung beetles, distributed along an agricultural landscape, to the three aforementioned types of radiation. We used a spectrophotometer to characterize the transmittance, reflectance and absorbance of the elytra to radiation with different wavelengths, to (I) derive common patterns, as well as (II) to examine the correspondence between these patterns and the species habitat preference along the agricultural landscape.

MATERIALS AND METHODS

Origin of specimens. Specimens come from a survey conducted in the region of São Miguel do Oeste, Santa Catarina (SC), southern Brazil (26°43′31″S, 53°31′05″W), in the summer of 2015. The surveyed area is an agricultural landscape composed mainly of maize crops with several patches of Atlantic Forest found within this agricultural matrix. Sampling was carried out at 30 sites—15 agricultural crop areas and 15 Atlantic Forest remnants. For each site, we placed five pitfall traps baited with human dung and five baited with decomposing pork meat, which were left in the field for 48 hours. All the collected insects were deposited in the entomological collection of the Federal University of Santa Catarina. Five *Canthon* species were selected for this study to minimize the occurrence of different responses due to phylogenetic differences, considering just diurnal species (20), and using a pool of species manifesting different environmental preferences (forest or maize crop areas). Thus, considering abundance data (Table S1), general habitat preferences were established according to the percentage of individuals collected within the forest and agricultural areas. Two species seemed to inhabit forest areas preferentially: *Canthon angularis* Harold, 1868 (99% of individuals), and *Canthon lividus lividus* Blanchard, 1845 (100%). Two other species preferentially inhabited open agricultural areas: *Canthon chalybaeus* Blanchard, 1845 (91%), and *Canthon tetraodon* Blanchard, 1845 (100%), while *Canthon quinquemaculatus* Castelnau, 1840, appeared in both forest (75%) and agricultural areas (25%). These species varied in dry body weight from 0.020 to 0.054 g and presented a blue–green coloration, except for *C. quinquemaculatus* that had orange–yellow coloration with black areas (Fig. 1).

Body measurements. A total of 45 specimens of the formerly mentioned species were analyzed (*n* = 10, 9, 10, 6 and 10 for *C. angularis*, *C. lividus lividus, C. chalybaeus, C. tetraodon* and *C. quinquemaculatus*, respectively). To evaluate whether reflectance, transmittance or absorbance rates are influenced by the morphological characteristics of the individuals, all were weighed using a Tx423L Shimadzu® balance with a precision of ± 0.001 g. Body thickness (BT), body width (BW) and body length (BL) were measured for each individual using a stereoscopic microscope (Fig. 1) to calculate their body volume as follows: $4/3 \times \pi \times BL \times BW \times BT$. Elytra thickness was also measured in its inner central part, and the three morphological variables (body weight, body volume and elytra thickness) were used as continuous covariates.

Spectrophotometric analysis. The left elytra of each individual were carefully removed with tweezers and placed in a Shimadzu® UV-2600 spectrophotometer to calculate both reflectance (R) and transmittance (T).

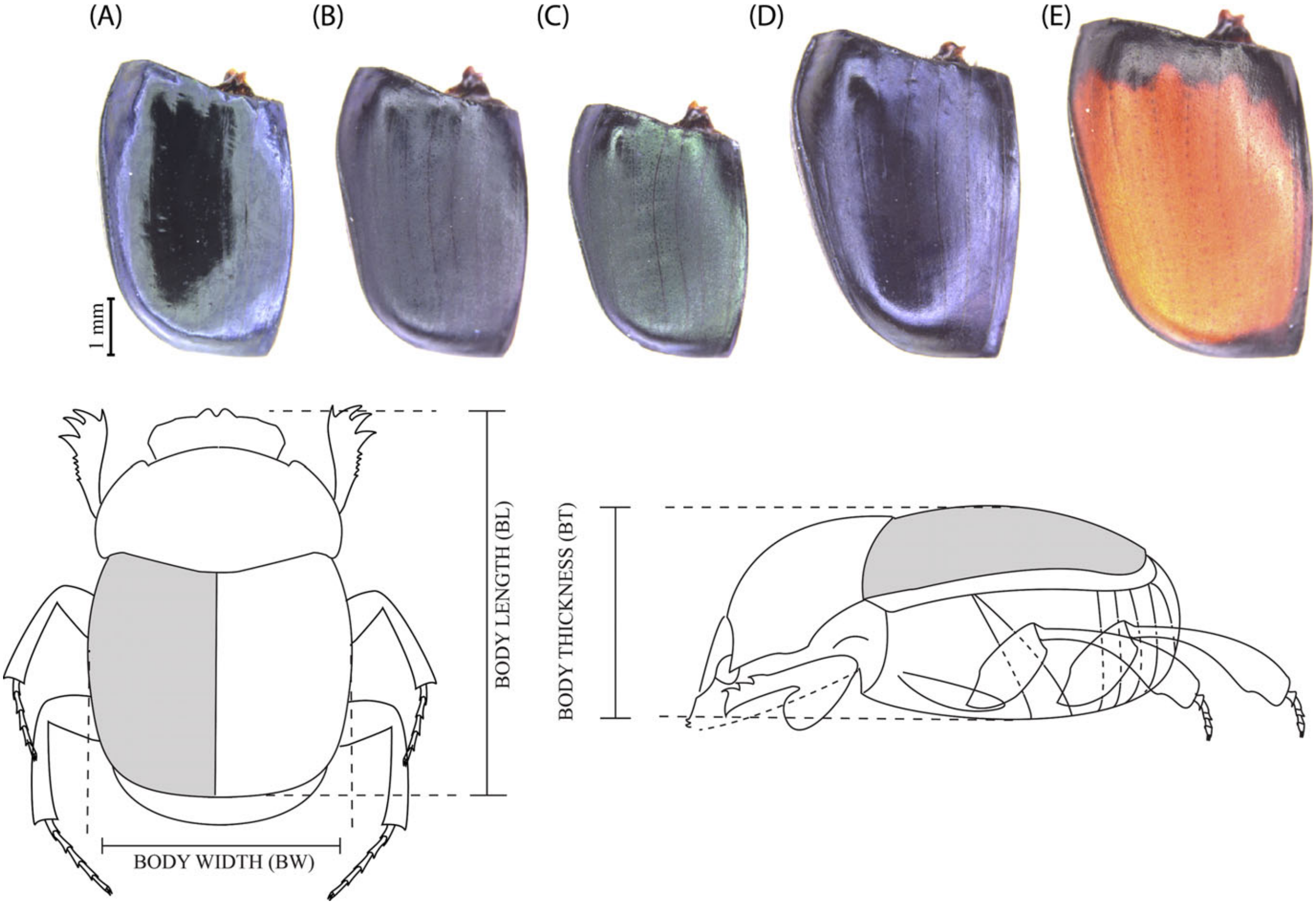

Figure 1. Elytra color variation of the five dung beetle species used in the study: (A) *Canthon angularis,* (B) *Canthon lividus lividus,* (C) *Canthon chalybaeus,* (D) *Canthon tetraodon* and (E) *Canthon quinquemaculatus*, and estimated dung beetle body measurements. The shaded region indicates the anatomical position of the elytra removed for analysis.

Absorbance (A) is estimated as 100-(R+T) (13). This spectrophotometer continuously scans the elytra surface with different monochromatic wavelengths ranging from 185 to 1400 nm at 10-nm intervals. Three scans were performed for each elytron. The coefficient of variation (CV) between these three measurements is very low both for transmittance (CV = 1.5%) and for reflectance (CV = 0.3%) or absorbance (CV = 0.2%). Thus, average values of T, R and A are calculated taking into account these three repetitions. The complete electromagnetic spectrum examined was divided into three ranges: ultraviolet (UV) from 185 to 390 nm, visible (VIS) from 391 to 749 nm and near infrared (NIF) from 750 to 1400 nm. Average T, R and A percentages are calculated for each one of the spectral ranges in all the individuals, and this percentage considered as the response variable in statistical analyses. In the specific case of NIF radiation, T, R and A are calculated both for the dorsal and ventral parts of the elytra to examine the possible elytral capacity of reflecting or transmitting the heat generated by the beetle's body (*i.e.* to evaluate whether there are different responses when the radiation reaches the body from an external heat source and when it tries to leave the body). To examine the influence of the elytra placement in the spectrophotometer, we changed this position three times in an individual of *C. quinquemaculatus* always obtaining the same pattern with CV values of 18% for transmittance, 6% for reflectance and 5% for absorbance. This influence was only examined in *C. quinquemaculatus* because the spectrophotometer ray reached almost entirely the elytra area of the other *Canthon* species.

Statistical analyses. General linear models (GLMs) with a type III sum of squares (*i.e.* estimating the partial effects of each factor while controlling for the effects of the remaining predictors) were used to estimate the differences between species in the percentages of transmittance, reflectance and absorbance for UV, VIS and NIF spectral ranges. "Species" was included as a fixed factor in all the analyses, while elytra side (dorsal *vs* ventral) was also a fixed factor in the case of NIF radiation. The three morphological variables (weight, volume and elytra thickness) were included as covariates following an ANCOVA model design. Type III sum of squares allows the calculation of the partial effect of the species factor while controlling for the effects of the morphological covariates (from now on named pure variability). The difference between this pure explained variability and the explanatory capacity of the species factor when included alone will be high when the two kinds of predictors covary. As the morphological characteristics of the individuals also form part of the distinctive morphology of the species, this explanatory difference can be attributed to the joint or inextricable effect of all the considered predictors. Model residuals were checked for normality and homoscedasticity assumptions. All statistics were performed using StatSoft's STATISTICA v12.0 (35).

RESULTS

The species present a similar pattern across the complete examined wavelength spectrum (Fig. 2). At higher wavelengths (NIF radiation), transmittance and absorbance are the major elytra responses. However, as the wavelength decreases, absorbance becomes the main elytra response (Fig. 2).

On average, UV and VIS transmittances are low (<2% and 7%, respectively), while reflectance percentages are similar, albeit modest (≈ 3%). Thus, most part of the UV and VIS radiation would be absorbed by the elytral cuticle (around 96% in the case of UV and 90% for VIS). However, although NIF dorsal reflectance continues to be moderate (≈ 11%), transmittance and absorbance percentages are relatively high (around 46% and 43%; see Table 1).

Ultraviolet (UV; 185–390 nm) and visible radiation (VIS; 391–749 nm)

Neither transmittance ($F_{(7,\ 37)} = 1.84$, $P = 0.11$) nor reflectance ($F_{(7,\ 37)} = 1.98$, $P = 0.08$), nor absorbance ($F_{(7,\ 37)} = 1.74$, $P = 0.13$) in the UV spectrum can be significantly explained by the considered predictors. This implies that the low UV transmittance and reflectance values as well as the high UV absorbance

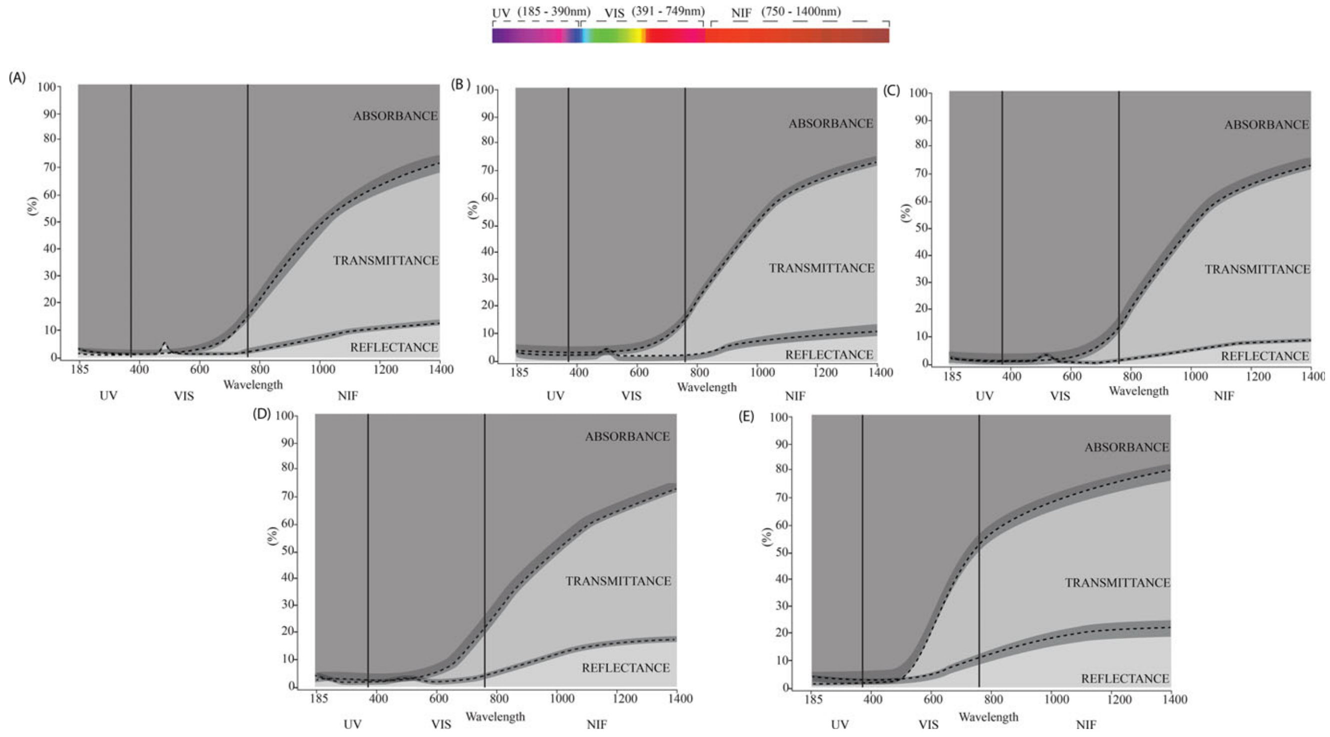

Figure 2. Absorbance, reflectance and transmittance percentages across the complete spectrum for the five considered dung beetle species: (A) *Canthon angularis*, (B) *Canthon lividus lividus*, (C) *Canthon chalybaeus*, (D) *Canthon tetraodon* and (E) *Canthon quinquemaculatus*. Shaded areas represent variation in the values obtained for the different individuals.

Table 1. Mean values (± 95% confidence interval) of absorbance (a), transmittance (t) and reflectance (r) measurements under near-infrared (NIF), visible (VIS) and ultraviolet (UV) radiation of the five considered species of dung beetles.

	Canthon angularis	*Canthon lividus lividus*	*Canthon chalybaeus*	*Canthon tetraodon*	*Canthon quinquemaculatus*
UV (a)	96.13 ± 0.96	94.19 ± 2.33	95.76 ± 1.27	95.96 ± 1.58	97.02 ± 0.09
UV (t)	1.27 ± 1.33	3.01 ± 1.40	1.57 ± 1.33	1.28 ± 1.71	0.04 ± 1.33
UV (r)	2.59 ± 0.15	2.80 ± 0.16	2.67 ± 0.15	2.75 ± 0.15	2.93 ± 0.15
VIS (a)	94.02 ± 1.25	92.17 ± 2.66	94.36 ± 1.12	92.11 ± 2.14	79.94 ± 2.48
VIS (t)	3.62 ± 1.89	5.37 ± 1.99	3.35 ± 1.89	5.20 ± 2.43	15.13 ± 1.89
VIS (r)	2.36 ± 0.23	2.46 ± 0.24	2.29 ± 0.23	2.69 ± 0.29	4.94 ± 0.23
NIF (a)	45.72 ± 2.17	45.17 ± 1.90	45.01 ± 3.18	41.36 ± 3.53	26.94 ± 4.18
NIF (t)	46.08 ± 2.44	45.55 ± 2.58	46.52 ± 2.44	45.34 ± 3.15	53.70 ± 2.44
NIF (r)	8.19 ± 0.99	9.27 ± 1.04	8.45 ± 0.99	13.29 ± 1.27	19.35 ± 1.04

Table 2. GLM results of transmittance, reflectance and absorbance values in the visible (VIS) wavelength spectrum (391–749 nm). Type III sum of squares was used in these analyses to estimate the partial effect of the species factor while controlling for the effects of the morphological covariates.

	Transmittance		Reflectance		Absorbance		
Variables	*F*	*P*	*F*	*P*	*F*	*P*	d.f.
Species	4.75	**0.003**	16.49	**<0.0001**	7.32	**0.0001**	4, 37
Weight	3.08	0.09	0.86	0.36	3.65	0.06	1, 37
Volume	6.80	**0.01**	1.87	0.18	8.06	**0.007**	1, 37
Elytra thickness	0.64	0.43	0.32	0.57	0.78	0.38	1, 37

Values in bold font highlight *P*-values ≤0.01.

percentages do not vary among the analyzed species. The considered morphological predictors (body weight, volume and elytra thickness, Table S2) do not interfere with UV radiation responses. Therefore, different morphologies (as well as different species) have the same pattern of reflectance, transmittance and absorption of UV radiation.

However, VIS transmittance, reflectance and absorbance variation are accounted for by the selected explanatory variables ($R^2 \times 100 = 75.9\%$, 91.6% and 83.1%, respectively). VIS transmittance values significantly vary between the considered species (Table 2), which is a factor able to explain around 12% of total variability independently of the considered morphological predictors (*i.e.* pure variability). As the variability accounted for by the factor species when considered alone is 71%, most (≈ 83%) of the explained variability in the VIS transmittance would be due to the joint or inextricable effect of all the considered predictors. A *posthoc* test indicates that the only statistically significant difference between the species is that of *C. quinquemaculatus* with the remaining species (Fig. 3A), where this species has higher transmittance values. Body volume barely explains 4.4% of total variability (higher transmittance at larger volumes).

VIS reflectance percentages also significantly differ between the species (Table 2), where its pure explained variability is 15.1%. Again, the variability accounted for by the species factor alone is very high (91%) so that mainly the joint effects of the factor species associated with their morphological characteristics must explain VIS reflectance. Furthermore, *posthoc* tests show that *C. quinquemaculatus* is the unique species with significantly high and different reflectance values (Fig. 3A). Lastly, VIS absorbance results show a similar pattern. The species factor (13.4% of total pure variability) and body volume (3.7%) are the only statistically significant predictors, where the individual explanatory capacity of the factor species is also very high (79%). The VIS absorbance values for *C. quinquemaculatus* are unique and significantly lower and different from those of other species (*posthoc* test).

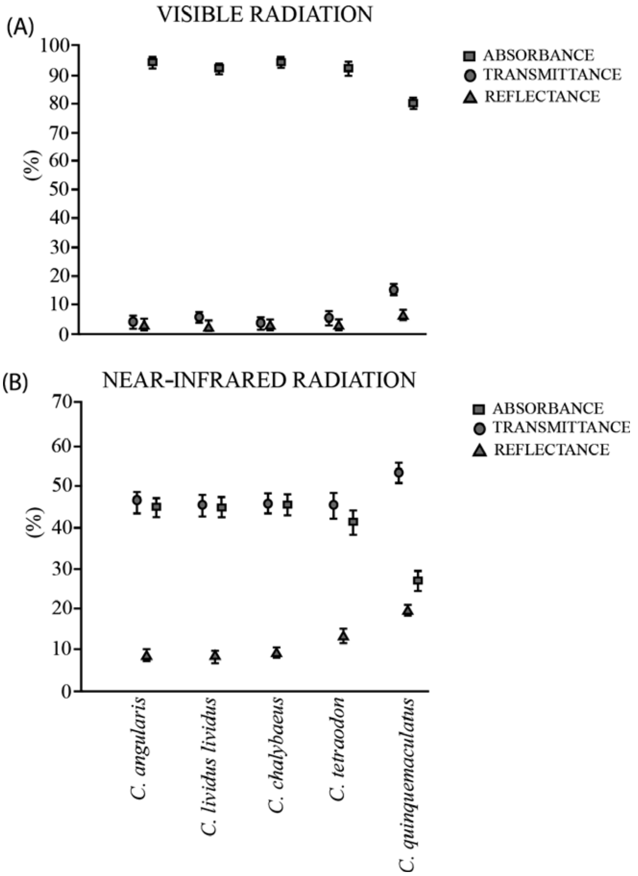

Figure 3. Absorbance (squares), transmittance (circles), reflectance (triangles) and adjusted mean values (± 95% CI) of the different species in the (A) visible electromagnetic spectrum and in the (B) near-infrared electromagnetic spectrum when all the considered predictors are held at their means (*i.e.* controlling for the effect of the three covariates included in the model; body weight, volume and elytra thickness).

Near-infrared radiation (NIF; 750–1400 nm)

Total NIF transmittance, reflectance and absorbance variation can be accounted for by the selected explanatory variables

Table 3. GLM results of transmittance, reflectance and absorbance values in the near-infrared (NIF) wavelength spectrum (750–1400 nm). Type III sum of squares was used in these analyses to estimate the partial effect of the species factor while controlling for the effects of the morphological covariates.

	Transmittance		Reflectance		Absorbance		
Variables	*F*	*P*	*F*	*P*	*F*	*P*	d.f.
Species	3.09	**0.02**	10.17	**<0.0001**	9.02	**<0.0001**	4, 77
Elytra side	5.85	**0.02**	5.02	**0.03**	12.26	**0.0008**	1, 77
Species*Elytra side	0.61	0.65	0.16	0.95	0.77	0.55	4, 77
Weight	4.76	**0.03**	4.14	**0.04**	10.01	**0.002**	1, 77
Volume	3.42	0.07	19.26	**<0.0001**	14.57	**0.002**	1, 77
Elytra thickness	0.42	0.52	2.72	0.10	1.91	0.17	1, 77

Values in bold font highlight *P*-values ≤ 0.02.

($R^2 \times 100 = 61.0\%$, 91.3% and 86.0%, respectively). NIF transmittance percentages vary between the considered species, the elytra side and the body weight (Table 3). However, as the interaction term "species * elytra side" is not statistically significant, the effect of the elytra side on NIF transmittance does not seem to vary among the considered species. The factor species is able to explain around 10% of total variability in NIF transmittance values independently of the considered morphological predictors. As the variability accounted for by the factor species is 25.8% when considered individually, more than half (≈ 60%) of the variability in NIF transmittance explained by the species factor would be due to the joint or inextricable effect of the considered predictors. *Posthoc* tests show that the only statistically significant differences between the species are those, which involve *C. quinquemaculatus* from the remaining species (Fig. 3B), as this species has a higher percentage of NIF transmittance. The elytra side accounted for 4.8% of the total NIF transmittance variability independent of the other predictors, being slightly higher on the ventral side (48.7% ± 1.7%; mean ± 95% CI) than on the dorsal side (45.9% ± 1.7%). The pure explanatory variability accounted for by body weight is 3.9%. As the three morphological variables are able to explain 20.5% of total variability in NIF transmittance, most of the explanatory capacity should be again assigned to the inseparable effect of the considered predictors.

NIF reflectance also varies between the species, the elytra side, the body weight and the volume (Table 3). The pure effect of the factor species accounts for 8.8% of the total variability. Again, the individual explanatory capacity of the factor species when considered alone is 73%, and most of the explained variability is due to the combined effect of the predictors. A *posthoc* test indicates that the statistically significant differences are due to the comparative higher NIF reflectance values of *C. tetraodon* and *C. quinquemaculatus* (Fig. 3B). Elytra side explains only 1% of the variability, where the reflectance is slightly higher in the ventral area (12.1% ± 0.7%) than in the dorsal area (11.0% ± 0.7%). Body weight also has an almost negligible explanatory capacity (hardly 1%), while body volume is able to explain 4% of total variability (higher NIF reflectance when the volume increases).

As a consequence of the former results, absorbance also differs between the considered species purely explaining 12.2% of total variability (57% when considered individually). *Posthoc* tests indicate that the low absorbance values of *C. quinquemaculatus* are significantly different from all the other species (Fig. 3B). The elytra side accounts for 4% of the total variability, while body weight and volume explain 4% and 5% of total variability.

DISCUSSION

This is the first study that evaluated the reflectance, absorbance and transmittance capacities of the elytra in Neotropical dung beetles. The obtained results indicate that the subtle morphological differences between the considered species have a relatively small explanatory capacity (≈4%) and that most of the differences between species in reflectance, absorbance and transmittance are accounted for by the combined effect of morphological and species identity variables. Thus, morphological characteristics of the individuals form part of the distinctive features of the species, and both types of variables exercise a combined effect in explaining the obtained patterns. Most importantly, the provided results also pinpoint that all the selected species show a relatively similar pattern: light of shorter wavelengths and higher frequencies is almost entirely absorbed, while radiation of longer wavelengths and lower frequencies can largely pass through the elytra.

Species did not show differences in the response to UV radiation. Thus, this highly energetic source of radiation is barely reflected and most of it is absorbed by the elytra (around 96%). Due to the serious damage that can be caused by the exposure to UV radiation, such as cell mutation (36), DNA damage (37) and metabolic stress (38), we expected that the elytra would reflect most of the UV radiation. Some insects have structures able to reflect UV radiation, such as Lepidoptera, in which this radiation is reflected by ultrastructures found in the wings (39). In the case of Coleoptera, Pope and Hinton (27) reported UV reflectance in several families (including Scarabaeidae), but this reflectance occurs in very specific body regions covered with setae and secretions. Other authors have suggested that the surface wax of insect cuticles would serve to reflect UV (40) and that elytra reticulation patterns could also reflect UV radiation (41). UV reflectance can be a negatively selected characteristic in the case of diurnal insects, such as *Canthon* species (20). Although UV reflectance seems to be used for communication in Lepidoptera, diurnal species that reflect this radiation attract predators, mainly birds (42,43). Birds can see ultraviolet light (44) and are predators of dung beetles (45). Thus, we suspect that the lack of UV reflectance in the studied species may be associated, at least partially, with protection against predation.

UV radiation and shorter visible wavelengths are in large part absorbed by the elytra. The absorption of the energy coming from a light with a shorter wavelength may be followed by the emission of light with a longer wavelength in the process known as fluorescence. Vulinec (46) showed that some Scarabaeinae species of the genus *Phanaeus* have areas that fluoresce under UV light, probably for sexual purposes. Other Coleoptera also absorb UV light and fluoresce, such as *Cteniopus sulphureus,* in which individuals reflect a strong yellow light (the complementary color of violet) when subjected to ultraviolet light (47). In any case, the elytra of the studied dung beetles of the genus *Canthon* do not reflect UV light or fluoresce when submitted both to a UV source of 380 and 254 nm (data not shown). What is the fate of this absorbed radiation? If absorbed energy does not generate fluorescence then a plausible possibility is that these photons excite the atoms in the elytra converting this energy into heat that may be further used in the thermoregulation process (48). Recent evidence shows that beetles reach higher internal body temperatures when submitted to artificial sunlight than under infrared radiation (49,50). However, it is necessary to design additional experiments to verify this supposition and to estimate the amount of body heat coming from the exposure to shorter wavelengths.

In the case of visible radiation, only *C. quinquemaculatus* seems to show a distinctive pattern associated with its distinctive coloration (see Fig. 2 and Figure S1). This species exhibits slightly higher transmittance and reflectance values than the other studied species, as well as higher reflectance values in the orange–red spectrum of visible light (from 590 to 750 nm). For the remaining species, the small observed peaks appear in the range from 400 to 500 nm (Figure S1) according to the blue–green coloration of *C. angularis*, *C. chalybaeus*, *C. lividus lividus* and *C. tetraodon*.

The different coloration observed in *C. quinquemaculatus* may be attributed to mimicry of a Hymenoptera pattern, and this mimicry may be linked with the thermoregulatory capacity of the elytra. Batesian mimicry is widely observed in insects and several species mimic dangerous bees and wasps. Mimetic species usually present a yellowish or orange color interspersed with black regions and frequently exhibit similar behavior. This mimicry has been described in Diptera (51), Coleoptera (52), Lepidoptera (53) and Neuroptera (54) but not in Scarabaeinae, although the coloration pattern of *C. quinquemaculatus* is convergent in several species of this genera, as well as in some species of other genera, including *Deltochilum*, *Scybalocanthon* and *Canthidium*.

The reflective capacity of the elytra seems to be an ancestral feature described for a 50-million-year fossil (55). In Coleoptera, reflectance patterns seem to be smaller under visible radiations (56), and only some beetles with metallic colors have high reflectance values (57). In our study, reflectance values are modest reaching a maximum of 20% across the entire spectrum, including visible color peaks (reaching 5% of reflectance).

Thus, the elytra of *Canthon* species seem to be opaque to UV and short visible wavelengths, but almost transparent to longer visible wavelengths and near-infrared radiation. A similar pattern has also been described for three Lepidoptera species (58). Furthermore, previous studies have shown that the initial body warm-up of dung beetle species would be passively facilitated by the permeability of the exoskeleton to infrared radiation (49,50). Consequently, thermal radiations can move in and out of the body, and beetles may acquire or eject the heat relatively easy. However, NIF transmittance seems to be comparatively higher in *C. quinquemaculatus* so that the cuticle of this species lets heat pass through much more so than other species. Interestingly, this elytral transparency to heat seems to be slightly higher from the inside independently of the species, suggesting that the elytral structure could comparatively better facilitate the removal of body heat. Additional morphological studies should be carried out studying the structure of the elytra exoskeleton to find the possible characteristics that generate these differences, and estimating the distribution of NIF transmittance values among dung beetle species.

Although provisional, there is not a clear correlation between the relative occurrence of the species in the two examined habitats and their elytral responses to the different radiation sources. Species with similar habitat preferences, such as *C. angularis* and *C. lividus lividus* in forest areas, and *C. chalybaeus* and *C. tetraodon* in agricultural areas, seem to manifest similar spectrophotometric responses. Only *C. quinquemaculatus*, a species that can inhabit in different kinds of habitats, shows a different pattern: both infrared and visible radiations with longer wavelengths can permeate their elytra in both sides thus heating its body or allowing the dissipation of body heat. Thus, this high transmittance could be associated with a faster acquisition of heat in conditions of low solar radiation, such as those under wooded environments or at dusk and dawn, but also be advantageous to avoid overheating in open areas (with more solar radiation) through the expulsion of internal body heat. Besides thermal advantage, the presence of *C. quinquemaculatus* in open areas may be favored by their protection against predation due to its bee-like coloration pattern. In any case, more studies comprising a higher number of species with contrasting environmental preferences are necessary to determine the correlation between spectrophotometric responses and the ecological or biogeographical characteristics of species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Visible spectral reflectance of the elytra of the different studied species.

Table S1. Abundance values collected for the five species of dung beetles in the surveyed forest fragments (FF) and maize crops (MC) within an agricultural landscape located in the region of São Miguel do Oeste, SC, Brazil.

Table S2. Mean values (± 95% confidence interval) of the morphological variables used as covariates for five dung beetles species.

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