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A Quantitative Analysis of Geographic Color Variation in Two Geotrupes Dung Beetles

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†Department of Zoology, Faculty of Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo-ku, Kyoto 606-8502, Japan,
‡Center for Ecological Research, Kyoto University, Kamitanakami Hiranocho, Otsu, Shiga 520-2113, Japan.

ABSTRACT—We conducted a quantitative analysis of geographic color variation in two species of dung beetles: Geotrupes auratus and G. laevistriatus. The reflectance of the dorsal surfaces was measured from 300 to 700 nm using a spectrophotometer. The reflectance curves for both beetles were bimodal; there were two distinct peaks, namely, the α peak, between 400 and 700 nm, and the β peak at around 300 nm. A stepwise discriminant analysis indicated that geographic color variation in Geotrupes beetles was primarily characterized by a shift of the α peak. Using beetles from three locations, we compared the wavelength (nm) of the α peak (λmax(α)) and its reflectance intensity (R(α)) to investigate sex and population differences. Intraspecific geographic variation in coloration was effectively detected by discriminant analysis of spectral reflectance curves. Our results showed that G. auratus and G. laevistriatus had similar coloration within each sampling location. Our study also revealed hidden sex differences in R(α); R(α) of males were significantly higher than those of females in both species. Since the dorsal surface of the beetles shows remarkable color variation, and coloration can be assessed objectively using reflectance spectra, Geotrupes beetles may be good model organisms to investigate geographic color variation.

Key words: dung beetle, reflectance spectra, geographic color variation, color measurement, sex difference

INTRODUCTION

As with many other morphological traits, animals can show dramatic geographic variation in coloration. Many different selective pressures, including thermoregulation, intraspecific communication, and predator avoidance, could generate this variation in color (Endler, 1978). Although researchers have long been interested in geographic color variation as a possible consequence of adaptation to local environments, the quantification and classification of the coloration of animals has been dependent on human perception. However, it is now recognized that using human vision to evaluate coloration could lead to erroneous conclusions (Bennet et al., 1994). If receivers of color stimuli, such as predators or individuals of the opposite sex, influence the evolution of coloration, we need to understand receiver visual perception. Many studies have shown that color vision among many taxa can be considerably different from that of humans in both the range of visible wavelengths and the mode of color information processing (Menzel and Backhaus, 1991; Jacobs, 1992; Brandt and Vorobyev, 1997; Vorobyev et al., 1998). Recently, mathematical models based on the physiological and psychophysical knowledge of animal vision have been developed and used for quantitative analysis of ‘apparent (observer-perceived) color’ (Vorobyev et al., 1998; Cuthill et al., 1999; Vorobyev & Menzel, 1999; Sumner and Mollon, 2000; Vorobyev et al., 2001). The results of these studies strongly suggest that we should not reduce spectral information to human standards, since such a reduction could result in a loss of critical color information. Therefore, objective methods for assessing color patterns are required, and should encompass the entire wavelength range of the receiver (Cuthill et al., 1999).

Another difficulty in evaluating animal coloration is that it often involves complex patterns. We usually do not have exact knowledge of which color components or combinations of color are ecologically important. Consequently, many researchers are still obliged to describe and categorize the color patterns of animals subjectively. Hence, studies of the evolution of geographic color variation in animals...
could benefit from the spectral information of an organism that has a simple, ideally monochromatic, coloration.

For the reasons mentioned above, some coleopteran insects may be good model subjects. Harris (1991) described color variation in the sand-burrowing beetle Chaerodes trachyscelides by using indices calculated by the CIELab system (CIE, 1978). He revealed that variation in the color of Chaerodes beetles matched the color of the sand of their resident beach. However, he only compared variation in the lightness component of the color.

Here, we report the geographic color variation of two dung beetles: Geotrupes auratus Motsch and G. laevistriatus Motsch. These two species range throughout most of the Japanese islands, feeding on the dung of mammals. These Geotrupes beetles may be good models for studying geographic color variation, as they show remarkable geographic color variation and have nearly monochromatic elytra. Preliminary geographic color variation in these two beetles has been described in an early study (Mizuno, 1964), which identified five color types for G. auratus and two color types for G. laevistriatus. Judgment of coloration, however, was based on human visual perception. In this paper, we attempt to establish an objective method for quantifying the coloration of monochromatic dung beetles. For this purpose, we calculated several variables from the reflectance spectra of the dorsal surface (elytra) of the beetles, and then isolated the parameter that most effectively characterized the geographic variation in the coloration. To our knowledge, this is the first study to evaluate the color of beetles objectively and examine geographic differences statistically.

**MATERIALS AND METHODS**

We chose three sampling sites (Arashiyama, Otowayama and Nara Park; Fig. 1) where distinct color types (red, green and indigo, respectively) of Geotrupes auratus have been observed (Mizuno, 1964). We collected male and female G. auratus and G. laevistriatus.
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RESULTS

General Patterns

There was no significant difference in total body length (TL) and thorax width (TW) between sexes within a population (Table 1). When pooling males and females, there was no significant difference in TL and TW among the three populations of Geotrupes auratus (Kruskal-Wallis test; H=1.674, p=0.4330 for TL; H=2.529, p=0.2824 for TW). In contrast, TL and TW of G. laevistriatus were significantly different among the three populations (Kruskal-Wallis test; H=26.541, p<0.0001 for TL; H=24.974, p<0.0001 for TW). Nonparametric multiple comparison tests (Dunn, 1964) revealed that both TL and TW of G. laevistriatus collected at Otowayama were significantly larger than those from the other two sites (TL: Arashiyama vs. Otowayama, Q=3.04, p<0.01; Arashiyama vs. Nara Park, Q=1.60, n.s.; Otowayama vs. Nara Park, Q=5.02, p<0.001, TW: Arashiyama vs. Otowayama, Q=2.93, p<0.05; Arashiyama vs. Nara Park, Q=1.60, n.s.; Otowayama vs. Nara Park, Q=4.88, p<0.001).

We found two different types of spectra that characterize the reflectance spectra of each species (Fig. 3; A–F: averaged data are shown in 10-nm increments). All the spectra measured were bimodal, with a reflectance peak between 400 and 700 nm (α peak), and another peak near 300 nm (β peak). The α peak of G. auratus corresponds to the maximum intensity of the spectra (Fig. 3; A–C), but that of G. laevistriatus is moderate, and lower than the β peak (Fig. 3; D–F). Since most β peaks are not real peaks, as mentioned in the methods, we focused on the wavelength (λmax(α)) and reflectance intensity of the α peak (R(α)) in the following analyses.

Sex differences

There were highly significant differences in the mean reflectance of spectra of G. auratus (Table 2); males showed overall higher reflectance than females. Males of G. laevistriatus also showed higher mean reflectance than females, except at the Otowayama site (Table 2). There were no significant differences in the minimum reflectance of spectra (MIN), except in G. auratus at the Otowayama site (Table 2).

There were no significant differences in λmax(α) between sexes within a population (Table 3). On the other hand, the reflectance intensities of males were significantly higher than those of females in each species (Table 3). We

### Table 1. Sampling sites, total body length (mm) and thorax width (mm) of the Geotrupes beetles. There was no significant difference between sexes within a population. Sample numbers are in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Total body length (Mean±SD mm)</th>
<th>Thorax width (Mean±SD mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Arashiyama Otowayama Nara Park</td>
<td>Arashiyama Otowayama Nara Park</td>
</tr>
<tr>
<td>Geotrupes auratus</td>
<td>Male</td>
<td>17.8±1.0 (18) 17.5±1.1 (26) 17.6±1.1 (42)</td>
<td>10.2±0.6 (18) 9.9±1.4 (26) 1.0±0.7 (42)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>18.6±1.2 (9) 17.4±0.7 (30) 17.5±2.0 (47)</td>
<td>10.4±0.6 (9) 10.0±0.7 (30) 10.0±0.6 (47)</td>
</tr>
<tr>
<td>Mann-Whitney test</td>
<td>p=0.1498</td>
<td>p=0.5323</td>
<td>p=0.5485</td>
</tr>
<tr>
<td>Geotrupes laevistriatus</td>
<td>Male</td>
<td>16.6±1.2 (16) 17.7±0.9 (23) 16.5±0.9 (24)</td>
<td>9.3±0.7 (16) 10.0±0.6 (23) 9.3±1.0 (24)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>16.9±1.0 (14) 17.6±0.9 (27) 16.3±1.1 (12)</td>
<td>9.6±0.6 (14) 9.9±0.5 (27) 9.0±0.7 (12)</td>
</tr>
<tr>
<td>Mann-Whitney test</td>
<td>p=0.5746</td>
<td>p=0.5924</td>
<td>p=0.5347</td>
</tr>
</tbody>
</table>
Fig. 3. Reflectance spectra of the dorsal surface of beetles. Figs. illustrate the mean and standard deviation in 10-nm increments for all the samples at each sampling site.

Table 2. Sexual differences in elytrons reflectance spectra. Sample numbers are in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Mean reflectance (average±SD)</th>
<th>Minimum reflectance (average±SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Arashiya</td>
<td>Otowayama</td>
</tr>
<tr>
<td><em>Geotrupes auratus</em></td>
<td>Male</td>
<td>8.7±0.5 (18)</td>
<td>8.4±0.5 (26)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>8.0±0.3 (9)</td>
<td>7.9±0.6 (30)</td>
</tr>
<tr>
<td>Mann-Whitney test</td>
<td></td>
<td>z=-3.240</td>
<td>z=-3.138</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p=0.0012</td>
<td>p=0.0017</td>
</tr>
<tr>
<td><em>G. laevistriatus</em></td>
<td>Male</td>
<td>6.5±0.3 (16)</td>
<td>6.4±0.3 (23)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>6.2±0.2 (14)</td>
<td>6.3±0.3 (27)</td>
</tr>
<tr>
<td>Mann-Whitney test</td>
<td></td>
<td>z=-2.785</td>
<td>z=-0.895</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p=0.0053</td>
<td>p=0.3706</td>
</tr>
</tbody>
</table>
also examined whether $R(\alpha)$ was related to the body length of males and females. However, no significant correlations were observed (data not shown).

**Population comparisons**

Since there were no significant differences in $\lambda_{\text{max}}(\alpha)$ between the sexes, we compared the $\lambda_{\text{max}}(\alpha)$ of different populations using combined (male and female) data. Fig. 4 shows the distribution of $\lambda_{\text{max}}(\alpha)$. Distributions of $\lambda_{\text{max}}(\alpha)$ were significantly different among populations (Kruskal-Wallis test; $H=140.310$, $p<0.0001$ in *G. auratus*; $H=59.966$, $p<0.0001$ in *G. laevistriatus*). Multiple comparison tests revealed significant differences among the three populations of *G. auratus*: Arashiyama vs. Otowayama, $Q=3.57$, $p<0.01$; Arashiyama vs. Nara Park, $Q=10.41$, $p<0.001$; Otowayama vs. Nara Park, $Q=8.51$, $p<0.001$. The $\lambda_{\text{max}}(\alpha)$ of *G. laevistriatus* also differed significantly among two of the populations: Arashiyama vs. Otowayama, $Q=6.8\times10^{-6}$ (16); $7.0\pm0.5$ (23); $7.1\pm0.4$ (24); Arashiyama vs. Nara Park, $Q=6.3\pm0.5$ (14); $6.7\pm0.5$ (27); $6.6\pm0.5$ (12); Otowayama vs. Nara Park, $Q=2.058$, $p=0.0146$; Otowayama vs. Nara Park, $Q=2.443$, $p=0.0039$; Nara Park vs. Nara Park, $Q=2.0$, $p=0.10$ (not significant). The $\lambda_{\text{max}}(\alpha)$ of *G. laevistriatus* was more variable than that of *G. auratus* at all three sites (at Arashiyama, coefficient of variation

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>$\lambda_{\text{max}}(\alpha)$ (Average±S.D.)</th>
<th>Reflectance efficiency (Average±S.D.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Arashiyama</td>
<td>Otowayama</td>
</tr>
<tr>
<td><em>Geotrupes auratus</em></td>
<td>Male</td>
<td>611.4±14.3 (18)</td>
<td>541.6±16.3 (26)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>616.9±9.7 (9)</td>
<td>540.3±13.9 (30)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>z=–1.34</td>
<td>p=0.1797</td>
</tr>
<tr>
<td><em>G. laevistriatus</em></td>
<td>Male</td>
<td>632.4±45.0 (16)</td>
<td>536.0±35.2 (23)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>659.6±30.2 (14)</td>
<td>538.3±52.6 (27)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>z=–1.581</td>
<td>p=0.1139</td>
</tr>
</tbody>
</table>

*Fig. 4.* Histogram of the distribution of $\lambda_{\text{max}}(\alpha)$ measured on the dorsal surface of *G. auratus* and *G. laevistriatus*. Data are categorized using 25 nm bins.
Fig. 5. The canonical discriminant scores CAN1 and CAN2 of the dorsal surface spectra of G. auratus (a) and G. laevistriatus (b). Discriminant analyses were conducted for each sex, since some variables showed sex differences.

Table 4. Parameters in the canonical discriminant analysis using stepwise method.

(a) Stepwise improvements of discrimination

<table>
<thead>
<tr>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilks’ λ</td>
<td>0.011</td>
<td>0.230</td>
<td>0.013</td>
<td></td>
<td></td>
<td>0.359</td>
<td>0.788</td>
<td></td>
<td>0.251</td>
<td>0.902</td>
<td></td>
</tr>
<tr>
<td>$\chi^2(P)$</td>
<td>364.1‡</td>
<td>119.6‡</td>
<td>357.7‡</td>
<td>118.2‡</td>
<td></td>
<td>61.0†</td>
<td></td>
<td>67.7‡</td>
<td>5.0 (ns)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eigenvalue(%)</td>
<td>19.1(85.1)</td>
<td>3.3(14.9)</td>
<td>17.5(84.5)</td>
<td>3.2(15.5)</td>
<td></td>
<td>1.2(81.7)</td>
<td>0.3(18.3)</td>
<td></td>
<td>2.6(96.0)</td>
<td>0.1(4.0)</td>
<td></td>
</tr>
</tbody>
</table>

Standardized canonical discriminant coefficients

<table>
<thead>
<tr>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
<th>Variable</th>
<th>CAN1</th>
<th>CAN2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{\max}(\alpha)$</td>
<td>0.669</td>
<td>0.421</td>
<td>0.670</td>
<td>-0.799</td>
<td></td>
<td>1.066</td>
<td>0.087</td>
<td></td>
<td>-1.140</td>
<td>0.216</td>
<td></td>
</tr>
<tr>
<td>$\lambda_{\max}(\beta)$</td>
<td>0.612</td>
<td>-0.278</td>
<td>0.571</td>
<td>0.786</td>
<td></td>
<td>R(β)</td>
<td>-0.460</td>
<td>0.966</td>
<td>R(β)</td>
<td>0.795</td>
<td>0.517</td>
</tr>
<tr>
<td>MIN</td>
<td>0.333</td>
<td>-0.588</td>
<td>MIN</td>
<td>0.402</td>
<td>0.349</td>
<td>R(β)</td>
<td>0.382</td>
<td>0.864</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R(β)</td>
<td>-0.029</td>
<td>0.527</td>
<td></td>
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</table>

‡: P<0.0001, †: P<0.001, ns: not significant (P>0.05).

(b) Canonical discriminant analysis

The canonical discriminant scores CAN1 and CAN2 of the dorsal surface spectra of G. auratus (a) and G. laevistriatus (b). Discriminant analyses were conducted for each sex, since some variables showed sex differences.
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(CV)=2.1 in G. auratus and 6.6 in G. laevistriatus; at Oto-
wayama, CV=2.8 in G. auratus and 8.4 in G. laevistriatus; and
at Nara Park, CV=3.2 in G. auratus and 12.4 in G. lae-
vistriatus.

The differences in the shapes of the spectra were sum-
marized by canonical discriminant analysis (Fig. 5a, 5b; Table 4a, 4b). A stepwise discriminant analysis of variance in
the entire dataset (six variables) reduced the number of
discriminating variables to 4 for male G. auratus, 3 for
female G. auratus, 2 for male G. laevistriatus, and 3 for
female G. laevistriatus (significance associated with Wilks’
\( \lambda \), \( p<0.05 \); Table 4a). Analyses revealed that \( \lambda \max(\alpha) \) was
the most efficient parameter for discriminating between
sampling sites in both species (Table 4a). This analysis was
able to discriminate between sampling sites for both male
and female G. auratus clearly (Wilks’ \( \lambda=0.011 \) for males;
Wilks’ \( \lambda=0.013 \) for females). Although \( \lambda \max(\beta) \) had a large
effect on CAN1 scores in the final model (Table 4b), a dis-
criminant function analysis using only \( \lambda \max(\alpha) \) was more
effective at discriminating between sampling sites (Wilks’ \( \lambda=0.082 \) for males; Wilks’ \( \lambda=0.078 \) for females). In comparison,
discrimination analyses between sampling sites for male
and female G. laevistriatus showed relatively poorer perfor-
mance (Wilks’ \( \lambda=0.359 \) for males; Wilks’ \( \lambda=0.251 \) for females).
The canonical scores of samples from Oto-
wayama and Nara Park largely overlapped, although sam-
ple from Arashiyama could be clearly discriminated from
those from the other two sites (Fig. 5b). The CAN1 scores for
G. laevistriatus were highly dependent on \( \lambda \max(\alpha) \)
(Table 4b), and the frequency distributions of \( \lambda \max(\alpha) \) of G.
laevistriatus from Otowayama and Nara Park actually
shared a wide wavelength range (Fig. 4).

**DISCUSSION**

Our study demonstrates that reflectance spectra are
useful for describing the monochromatic color of the dorsal
surface of two dung beetle species, Geotrupes auratus and
G. laevistriatus. Furthermore, we show that geographic color
variation in each species is well characterized by the shift of
\( \alpha \) peaks. Since structural colors in the Geotrupes beetles
seem to be produced by a multilayer reflector, the \( \alpha \) peak of
reflectance may depend on the thickness of the layers in a
stack (Parker et al., 1998). Therefore, it seems appropriate to
use \( \lambda \max(\alpha) \) as an index for evaluating color variation in
Geotrupes beetles. Our analyses of \( \lambda \max(\alpha) \) also revealed
hidden (imperceptible by humans) sexual dichromatism in
both beetles; the reflectance intensity of males was signifi-
cantly higher than that of females at \( \lambda \max(\alpha) \). Through
objective spectral measurements, we may find hidden sex-
ual dichromatism in many other species.

Recently, Faviola et al. (2000) clearly demonstrated that
cuticular color in a Scarabaeinae beetle (Canthon cyanellus
cyanellus LeConte) is genetically controlled. If the coloration
of G. auratus and G. laevistriatus is also genetically con-
trolled, we should pay more attention to the frequency dis-
tribution of \( \lambda \max(\alpha) \) of a population. Coefficients of variation
in \( \lambda \max \) show that the coloration of G. auratus is more uni-
form than that of G. laevistriatus in all three populations.
Furthermore, the frequency distributions of \( \lambda \max(\alpha) \) in G.
laevistriatus largely overlap between the different sites. Dif-
ferences in the degree of variation within a population may
be explained by the differing levels of gene flow between the
two beetle species. Habitats of G. auratus to be restricted to
localized areas where wild mammals are more abundant,
while G. laevistriatus are observed more widely, even in iso-
lated green spaces within cities (Mizuno, 1964). Therefore,
gene flow among G. auratus populations seems to be more
restricted than in G. laevistriatus. Differences in the strength
of selective pressures may also explain the differences in
the degree of geographic variation within each species if the
coloration of the beetles is determined by natural or sexual
selection; selective pressures may be greater on G. auratus
than on G. laevistriatus in a specific area. To understand
these patterns of geographic variation, we need to deter-
mine the selective forces acting on the coloration, the level
of gene flow between populations, and the interaction
between these two selective pressures.

Interestingly, our results show that G. auratus and G.
laevistriatus share similar coloration in each habitat. Al-
though the coloration of G. laevistriatus appears dull to
human observers, spectral analyses reveal that the \( \alpha \) peaks
of G. laevistriatus shift in the same direction as those of G.
auratus. Additional populations should be surveyed to
understand the patterns in geographic color variation in
these two dung beetles.

Geographic color variation in G. auratus and G. laevis-
triatus does not appear to be maintained by thermoregula-
tion, since coloration does not vary with latitude (Mizuno,
1964). Alternatively, coloration might serve a function in
intraspecific communication, since there are sex differences
in the reflectance intensity of the \( \alpha \) peak. However, an
intraspecific signal function does not explain the similarity
of the coloration between the two Geotrupes beetles at each
site. If the dung beetles are unpalatable to predatory ani-
mal, and the coloration functions as a warning signal, the
color similarities between the two beetle species might be
explained by Müllerian mimicry, since they share the same
resources (the dung of mammals) and are frequently
observed together in the same habitat. Studies of the diurnal
activity of the beetles revealed that G. auratus and G. lae-
vistriatus activities peak in the daytime (Sasayama et al.,
1984). Therefore, their coloration may act as warning sig-
als for visual diurnal predators, such as birds. Pluot-Sigwalt
(1982, 1984) has demonstrated that some African dung
beetles in the tribe Gymnopleurini have exceptionally
numerous pygidial glands that generally secrete repellent
substances. The bright color of these beetles may be inter-
preted as warning colors (Camberfort, 1991). To our knowl-
edge, however, there is no evidence demonstrating the
unpalatability of the two Geotrupes dung beetles.

In conclusion, our quantitative analysis effectively eval-
uated the coloration of two dung beetles: *G. auratus* and *G. laevistriatus*. Using the objective index, \( \lambda_{\text{max}} \), we can compare the geographic color variation of the beetles quantitatively. We found coloration similarity between *G. auratus* and *G. laevistriatus* within sampling locations, and also hidden sex differences in the reflectance intensity of the beetles. The *Geotrupes* beetles may be an ideal model system for investigating causal factors of geographic variation in animal color patterns.

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