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Authors: Watanabe, Takashi, Tanigaki, Taketo, Nishi, Hirotaka, Ushimaru, Atushi, and Takeuchi, Tsuyoshi

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

Takashi Watanabe*[1], Taketo Tanigaki[1], Hirotaka Nishi[1], Atushi Ushimaru[2]
and Tsuyoshi Takeuchi[1]

[1] *Department of Zoology, Faculty of Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo-ku,*
Kyoto 606-8502, Japan,
[2] *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 ($\lambda\text{max}(\alpha)$) and its reflectance intensity ($R(\alpha)$) 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 $R(\alpha)$; $R(\alpha)$ 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 rariation, color measurement, sexdifference

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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 (Bennent *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

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* Corresponding author: Tel. +81-75-753-4077;
FAX. +81-75-753-4101.
E-mail: takeshi@ecol.zool.kyoto-u.ac.jp

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. laevistria-*

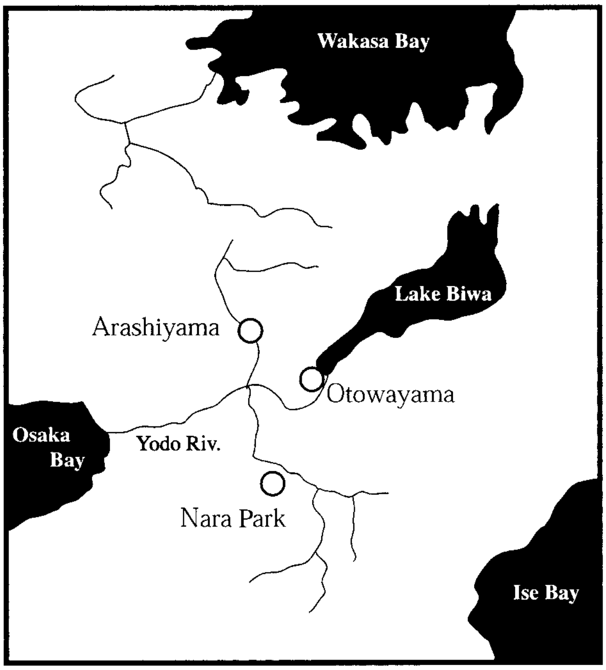

Fig. 1. Map of central Japan showing the positions of the sites from which samples were collected.

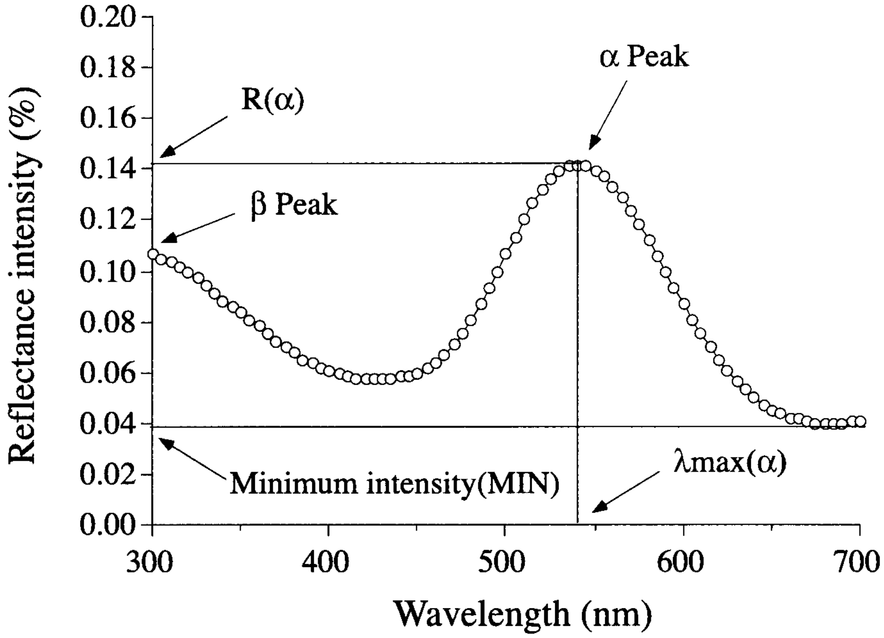

Fig. 2. Representative reflectance spectra of the dorsal surface of two species of dung beetle. Variables extracted from the spectral data (81 points from 300 to 700 nm in 5-nm increments) include α and β peak wavelength (λmax(α) and λmax(β), respectively), reflectance intensity (R(α) and R(β), respectively), mean intensity, and minimum intensity (MIN).

tus with baited traps using the dung of horses. We also collected the beetles from the dung of unknown mammals found at the study sites. The sampling was conducted from early May to mid August 2001. We measured total body length and thorax width in the laboratory.

We measured the reflectance spectra of the dorsal surface of beetles with a Shimadzu spectrophotometer UV-240, which measures wavelength with an accuracy of 0.3 nm. In our analyses, we used the reflectance data in the range from 300 to 700 nm, in 5-nm increments. We used a deuterium light source with the spectrophotometer, and barium sulfate (Merck) as a white standard. Since the coloration of the beetles appears to be of structural origin, it should change according to the viewing angle. In this study, the measurement angle of reflectance was perpendicular to the dorsal surface. In addition, there appears to be color variation among different parts of the body. Therefore, we only measured the coloration of the dorsal surface (elytra), which occupies the largest part of the body, although other parts, such as the underside and legs of the beetles also show geographic color variation (Watanabe, personal observation).

Before measuring all the samples, we conducted pilot studies and found that spectra are usually bi-modal within the measured wavelength range (see Fig. 2 for representative spectra), with a peak (α peak) within the range of human visual sensitivity (400–700 nm), and another peak (β peak) near 300 nm. Although most β peaks are not real peaks (they show the upper limit of an increasing phase toward the shortest wavelength measured), we treat them as such for convenience.

Six variables were obtained from the reflectance spectra: the wavelength corresponding to the α and β peaks ($\lambda\max(\alpha)$ and $\lambda\max(\beta)$, respectively), the reflectance intensity of the α and β peaks ($R(\alpha)$ and $R(\beta)$, respectively), as well as the mean and minimum reflectance (Fig. 2). The mean reflectance was calculated as the average reflectance of the entire spectrum measured in 5-nm increments (300–700 nm; n=81). The minimum reflectance (MIN) was the minimum value of the reflectance intensity. We used these parameters to examine sexual and geographic differences in coloration within each species. These variables were not normally distributed; consequently, we used a nonparametric statistical test for our analyses. In an attempt to discriminate between collection sites based on color variation, we used a canonical discriminant analysis, which included all six color parameters. To determine the order of effectiveness of these variables in discriminating between collection sites, we adopted a stepwise method for the discriminant analysis.

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 ($\lambda\max(\alpha)$) and reflectance intensity of the α peak ($R(\alpha)$) 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 $\lambda\max(\alpha)$ 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.

Species	Sex	Total body length (Mean±SD mm)			Thorax width (Mean±SD mm)		
		Arashiyama	Otowayama	Nara Park	Arashiyama	Otowayama	Nara Park
Geotrupes auratus	Male	17.8±1.0 (18)	17.5±1.1 (26)	17.6±1.1 (42)	10.2±0.6 (18)	9.9±1.4 (26)	1.0±0.7 (42)
	Female	18.6±1.2 (9)	17.4±0.7 (30)	17.5±2.0 (47)	10.4±0.6 (9)	10.0±0.7 (30)	10.0±0.6 (47)
Mann-Whiteny test		z=–1.44 p=0.1498	z=–0.624 p=0.5323	z=–0.600 p=0.5485	z=–0.772 p=0.4403	z=–0.608 p=0.5432	z=–0.012 p=0.9902
G. laevistriatus	Male	16.6±1.2 (16)	17.7±0.9 (23)	16.5±0.9 (24)	9.3±0.7 (16)	10.0±0.6 (23)	9.3±1.0 (24)
	Female	16.9±1.0 (14)	17.6±0.9 (27)	16.3±1.1 (12)	9.6±0.6 (14)	9.9±0.5 (27)	9.0±0.7 (12)
Mann-Whiteny test		z=–0.561 p=0.5746	z=–0.535 p=0.5924	z=–0.621 p=0.5347	z=–1.102 p=0.2706	z=–0.662 p=0.5080	z=–0.235 p=0.8143

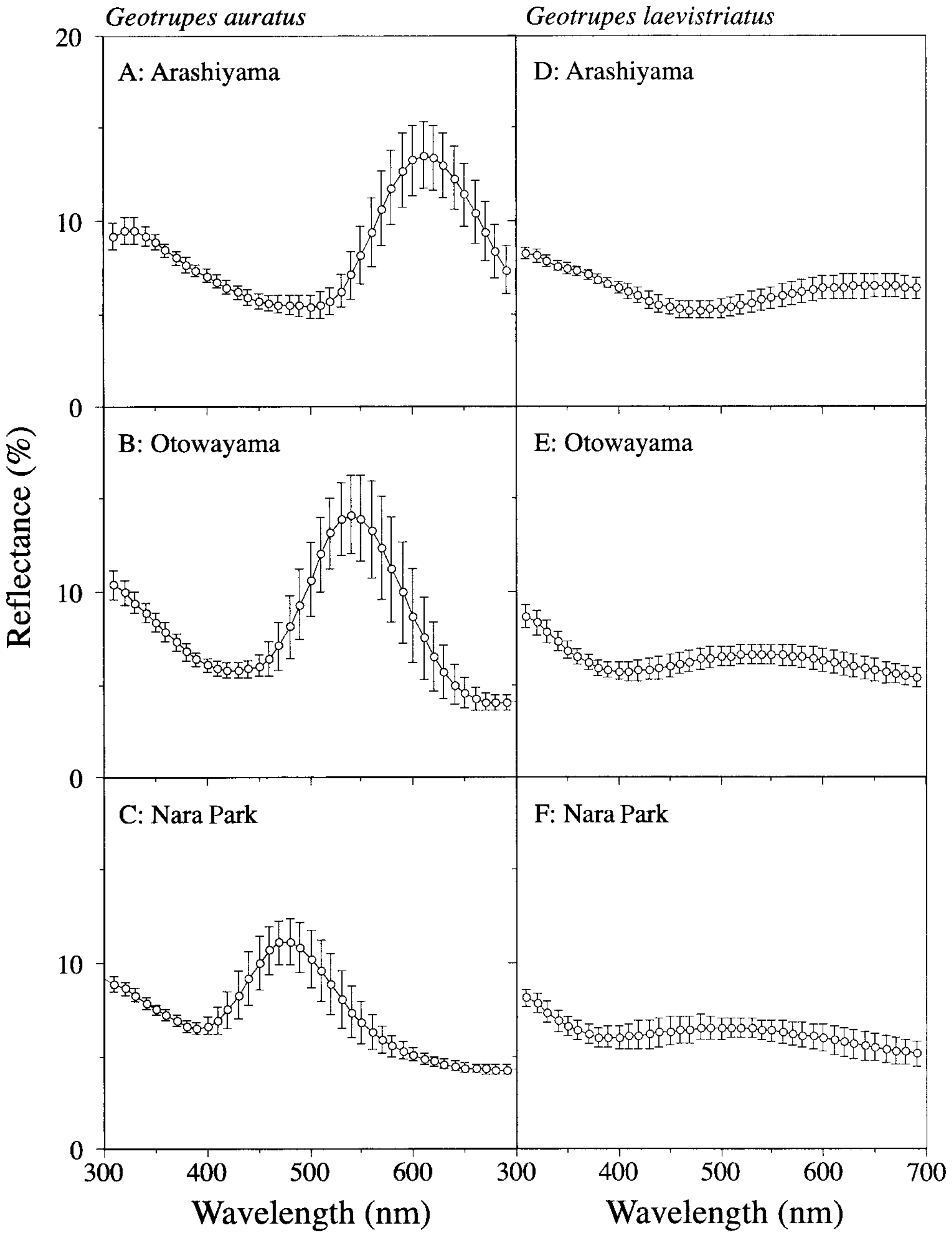

Fig. 3. Reflectance spectra of the dorsal surface of beetles. Figs. illustrate the mean and standard deviation in 10-nm increments for all the samples at each sampling site.

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

Species	Sex	Mean reflectance (average±SD)			Minimum reflectance (average±SD)		
		Arashiyama	Otowayama	Nara Park	Arashiyama	Otowayama	Nara Park
Geotrupes auratus	Male	8.7±0.5 (18)	8.4±0.5 (26)	7.3±0.3 (42)	5.2±0.6 (18)	3.6±0.3 (26)	4.3±0.3 (42)
	Female	8.0±0.3 (9)	7.9±0.6 (30)	7.0±0.3 (47)	5.1±0.5 (9)	4.0±0.4 (30)	4.2±0.2 (47)
Mann-Whiteny test		z=–3.240	z=–3.138	z=–4.107	z=–0.129	z=–3.894	z=–1.622
		p=0.0012	p=0.0017	p<0.0001	p=0.8977	p<0.0001	p=0.1049
G. laevistriatus	Male	6.5±0.3 (16)	6.4±0.3 (23)	6.3±0.3 (24)	5.2±0.5 (16)	5.0±0.3 (23)	4.9±0.4 (24)
	Female	6.2±0.2 (14)	6.3±0.3 (27)	6.1±0.2 (12)	4.9±0.5 (14)	5.1±0.3 (27)	4.8±0.3 (12)
Mann-Whiteny test		z=-2.785	z=–0.895	z=–2.248	z=–1.413	z=–1.392	z=–0.185
		p=0.0053	p=0.3706	p=0.0246	p=0.1575	p=0.1640	p=0.8536

Table 3. The λmax(α) (nm) and reflectance intensity (%) of α peaks with distinct of sex. Sample numbers are in parentheses.

Species	Sex	λmax(α) (Average±S.D.)			Reflectance efficiency (Average±S.D.)		
		Arashiyama	Otowayama	Nara Park	Arashiyama	Otowayama	Nara Park
Geotrupes auratus	Male	611.4±14.3 (18)	541.6±16.3 (26)	476.4±16.6 (42)	14.7±1.5 (18)	16.1±1.3 (26)	12.4±1.3 (42)
	Female	616.9± 9.7 (9)	540.3±13.9 (30)	474.5±14.5 (47)	12.1±1.2 (9)	13.6±1.9 (30)	11.0±0.9 (47)
Mann-Whiteny test		z=–1.34	z=–0.420	z=-0.169	z=–3.527	z=–4.699	z=–5.396
		p=0.1797	p=0.6747	p=0.8660	p=0.0004	p<0.0001	p<0.0001
G. laevistriatus	Male	632.4±45.0 (16)	536.0±35.2 (23)	507.2±63.2 (24)	6.8±0.6 (16)	7.0±0.5 (23)	7.1±0.4 (24)
	Female	659.6±30.2 (14)	538.3±52.6 (27)	502.5±63.7 (12)	6.3±0.5 (14)	6.7±0.5 (27)	6.6±0.5 (12)
Mann-Whiteny test		z=–1.581	z=–0.565	z=-0.235	z=–2.058	z=–2.443	z=–2.886
		p=0.1139	p=0.5720	p=0.8140	p=0.0396	p=0.0146	p=0.0039

also examined whether R(α) 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 λmax(α) between the sexes, we compared the λmax(α) of different populations using combined (male and female) data. Fig. 4 shows the distribution of λmax(α). Distributions of λmax(α) 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 λmax(α) of *G. laevistriatus* also differed significantly among two of the populations: Arashiyama vs. Otowayama, Q=6.08, p<0.001; Arashiyama vs. Nara Park, Q=7.44, p<0.001; Otowayama vs. Nara Park, Q=2.00, p>0.10 (not significant). The λmax(α) of *G. laevistriatus* was more variable than that of *G. auratus* at all three sites (at Arashiyama, coefficient of variation

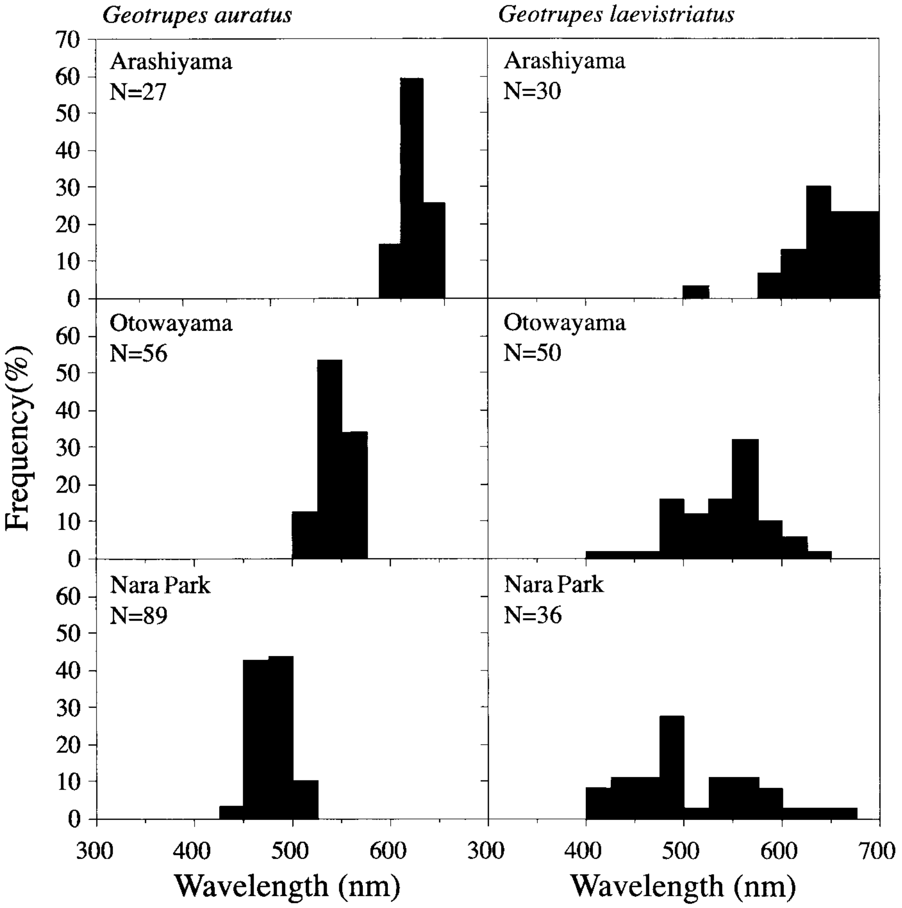

Fig. 4. Histogram of the distribution of λmax(α) measured on the dorsal surface of *G. auratus* and *G. laevistriatus*. Data are categorized using 25 nm bins.

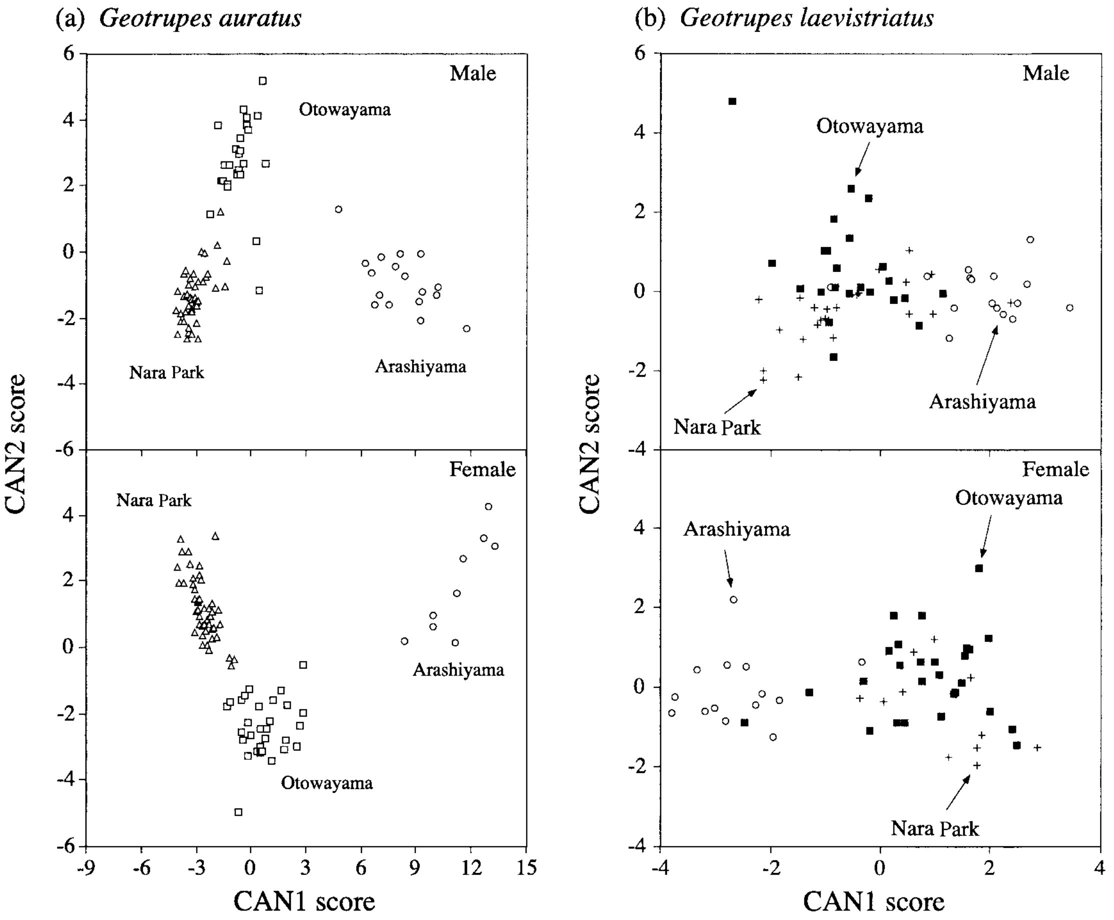

Fig. 5. The canonical discriminant scores CAN1 and CAN2 of the dorsal surface spectra of *G. auratus* (a) and *G. laevistriatus* (b). Discriminant analyses were conducted for each sex, since some variables showed sex differences.

Table 4. Parameters in the canonical discriminant analysis using stepwise method.
(a) Stepwise improvements of discrimination

G. auratus (male)			*G. auratus* (female)			*G. laevistriatus* (male)			*G. laevistriatus* (female)		
Step[#1]	Variable	Wilks' λ	Step	Variable	Wilks' λ	Step	Variable	Wilks' λ	Step	Variable	Wilks' λ
1	λmax(α)	0.082	1	λmax(α)	0.078	1	λmax(α)	0.494	1	λmax(α)	0.415
2	λmax(β)	0.022	2	λmax(β)	0.017	2	R(β)	0.359	2	λmax(β)	0.299
3	MIN	0.014	3	MIN	0.013				3	R(β)	0.251
4	R(β)	0.011									

#1: Variables are additionally entered into the model if probability of F value is smaller than 0.05.

(b) Canonical discriminant analysis

	G. auratus (male)			*G. auratus* (female)			*G. laevistriatus* (male)			*G. laevistriatus* (female)	
Variable	CAN1	CAN2	Variable	CAN1	CAN2	Variable	CAN1	CAN2	Variable	CAN1	CAN2
Wilks' λ	0.011	0.230		0.013	0.237		0.359	0.788		0.251	0.902
$\chi^2(P)$	364.1‡	119.6‡		357.7‡	118.2‡		61.0‡	14.1†		67.7‡	5.0 (ns)
Eigenvalue(%)	19.1(85.1)	3.3(14.9)		17.5(84.5)	3.2(15.5)		1.2(81.7)	0.3(18.3)		2.6(96.0)	0.1(4.0)
Standardized canonical discriminant coefficients											
λmax(α)	0.669	0.421	λmax(α)	0.670	−0.799	λmax(α)	1.066	0.087	λmax(α)	−1.140	0.216
λmax(β)	0.612	−0.278	λmax(β)	0.571	0.786	R(β)	−0.460	0.966	λmax(β)	0.795	0.517
MIN	0.333	−0.588	MIN	0.402	0.349				R(β)	0.382	0.864
R(β)	−0.029	0.527									

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

(CV)=2.1 in *G. auratus* and 6.6 in *G. laevistriatus*; at Otowayama, 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. laevistriatus*).

The differences in the shapes of the spectra were summarized 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' λ, $p<0.05$; Table 4a). Analyses revealed that λmax(α) 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' λ=0.011 for males; Wilks' λ=0.013 for females). Although λmax(β) had a large effect on CAN1 scores in the final model (Table 4b), a discriminant function analysis using only λmax(α) was more effective at discriminating between sampling sites (Wilks' λ= 0.082 for males; Wilks' λ=0.078 for females). In comparison, discrimination analyses between sampling sites for male and female *G. laevistriatus* showed relatively poorer performance (Wilks' λ=0.359 for males; Wilks' λ=0.251 for females). The canonical scores of samples from Otowayama and Nara Park largely overlapped, although samples 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 λmax(α) (Table 4b), and the frequency distributions of λmax(α) 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 α peaks. Since structural colors in the *Geotrupes* beetles seem to be produced by a multilayer reflector, the α peak of reflectance may depend on the thickness of the layers in a stack (Parker *et al.*, 1998). Therefore, it seems appropriate to use λmax(α) as an index for evaluating color variation in *Geotrupes* beetles. Our analyses of λmax(α) also revealed hidden (imperceptible by humans) sexual dichromatism in both beetles; the reflectance intensity of males was significantly higher than that of females at λmax(α). Through objective spectral measurements, we may find hidden sexual dichromatism in many other species.

Recently, Favila *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 controlled, we should pay more attention to the frequency distribution of λmax(α) of a population. Coefficients of variation in λmax show that the coloration of *G. auratus* is more uniform than that of *G. laevistriatus* in all three populations. Furthermore, the frequency distributions of λmax(α) in *G. laevistriatus* largely overlap between the different sites. Differences 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 isolated 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 determine 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. Although the coloration of *G. laevistriatus* appears dull to human observers, spectral analyses reveal that the α 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. laevistriatus* does not appear to be maintained by thermoregulation, 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 α 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 animals, 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. laevistriatus* activities peak in the daytime (Sasayama *et al.,* 1984). Therefore, their coloration may act as warning signals 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 interpreted as warning colors (Camberfort, 1991). To our knowledge, however, there is no evidence demonstrating the unpalatability of the two *Geotrupes* dung beetles.

In conclusion, our quantitative analysis effectively evaluated the coloration of two dung beetles: *G. auratus* and *G. laevistriatus*. Using the objective index, λmax, 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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