Character Displacement in Stag Beetles (Coleoptera: Lucanidae)

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ABSTRACT I quantitatively analyzed male morphology of two closely related stag beetles species (*Odontolabis mouhoti* Hope and *O. cuvera* Parry) in 11 allopatric and two sympatric locations in the Asian tropics and subtropics. Across allopatric locations, body size and genitalia size nearly completely overlapped between *O. mouhoti* and *O. cuvera*, and body color was more similar between the two species in allopatric locations. In sympatric locations the differences between the two species in these characters were highly noticeable, genitalia size being most significant. The body color difference between the two species was most striking in sympatric locations. It is probable that the interaction between the two species induced character displacement in sympatry. Character displacement may enable species to maintain themselves as integrated units by minimizing interspecific competition and enhancing reproductive isolation.

KEY WORDS character displacement, sympatry, allopatry, stag beetles, genitalia size, body size

THE EFFECTS OF INTERSPECIFIC interaction or competition on the phenotypes and genotypes of given species has been an important topic in evolutionary biology. There has been considerable discussion of how one interacting species dominates the other species in common habitat (e.g., Roughgarden 1983), or how interacting species adapt to mutual existence (e.g., Losos 1990). It is generally understood that interacting species can coexist when they are using different resources or are adapted to different conditions within the same area. It is frequently observed that when closely related species occur in sympatry, they are subtly different from each other in microhabitat, such as elevation (e.g., Diamond 1970), or in external morphology, such as beak size in birds (e.g., Lack 1947). This suggests that they are effectively differentiating the mode of resource use. This often has been interpreted as a result of natural selection for reducing interspecific competition (Grant 1972, 1981). However, whether the species differentiated as a result of interspecific interaction or adapted to different conditions independent of competition often cannot be determined (Grant 1972, Simberloff and Boecklen 1981, Simberloff 1983, Connor and Simberloff 1986, Losos 1990).

When habitat use of one species differs from that of a competing species in sympatry where they are interacting with each other, but is overlapping in allopatry where they are not interacting, the difference is sometimes hypothesized to have been caused by interspecific interaction (e.g., Hairston 1951 in salamanders, Diamond 1970 in New Guinean birds). This resource specialization in some cases leads to morphological differentiation or character displacement, which is recognized when the morphological difference between two interacting species in sympatry is greater than that between the species in allopatry (Grant 1972, 1981).

However, it is not easy to unambiguously establish that the character state of one population in sympatry is influenced by the presence of a coexisting, ecologically similar species (Dunham et al. 1979). Aside from the true effects of sympatry or interaction with other ecologically similar species, there are numerous factors that can affect the character states of populations (Schoener 1982). Examining scattered cases of alleged character displacement, Futuyma (1986) identified three prerequisites for confirming the existence of character displacement caused by species interaction in sympatry: character state in sympatry (when competing with other species) different from that in allopatry (when not competing), character difference between two species in sympatry larger than it is in allopatry; and allopatry/sympatry effect clearly separable from random ecological effects. Species to be studied for character displacement must be similar in morphology and behavior, and desirably close to each other phylogenetically but distant from other species in the same habitat. Such species must be distributed both allopatrically and sympatrically. There are few cases, if any, where all of these conditions have been met and the results supported by rigorous statistical tests.

In a previous study with two rhinoceros beetle species, *Chalcosoma atlas* L. and *C. caucasus* F., I detected a clear case of sympatric character displacement satisfying the conditions above beyond any statistical doubt (Kawano 2002). Similar cases of character dis-

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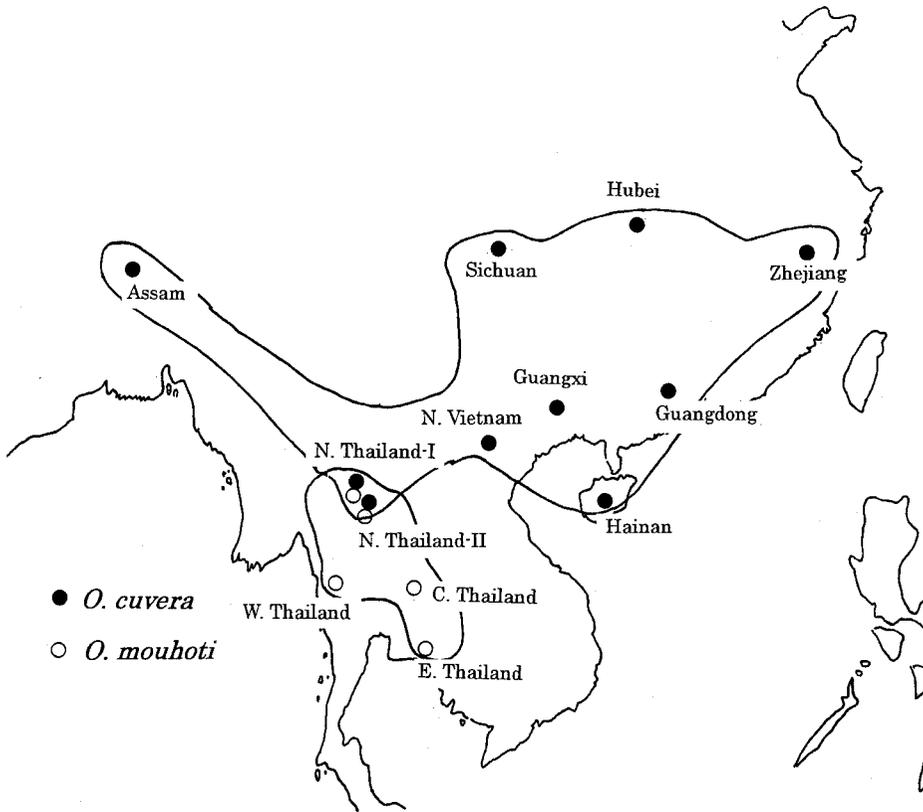
Fig. 1. Geographic distribution of allopatric and sympatric sites for *O. mouhoti* and *O. cuvera*, where sampling for this study was successful.

placement may be expected in the stag beetle family Lucanidae, which is taxonomically close to Scarabaeidae to which rhinoceros beetles belong. *Odontolabis mouhoti* Parry and *O. cuvera* Hope are widely distributed in the Asian tropics and subtropics. In most localities only one of the two species occurs, but in some locations in northern Thailand both species occur sympatrically. In allopatric locations, the two species are similar in body size and in some cases color as well. In sympatric locations they are less similar. Species of *Odontolabis,* like *Chalcosoma,* are known to show not only a remarkable sexual dimorphism, but also a rich intraspecific variation in the male, of which large variability of body size and extreme allometric variation of mandibles are the main features.

In this study I analyzed the male body size, mandible length, and, more importantly with respect to reproductive isolation as a possible cause of sympatric character displacement, the male genitalia size of the two *Odontolabis* species, using large population samples in 11 allopatric and two sympatric locations. I argue the case for sympatric character displacement in Lucanidae, and describe the biological nature of species interaction.

Materials and Methods

Species Studied. Many species and genera of Lucanidae with different morphologies and behaviors are distributed throughout Asia, among which *Odontolabis mouhoti* Hope and *O. cuvera* Parryi were selected as the most appropriate pair for studying sympatric character displacement in Lucanidae. They share many morphological features, especially the male intraspecific polymorphic pattern of mandibles and the nonsymmetric mandibles in small to medium size males, making them taxonomically, and probably phylogenetically, sister species. *O. mouhoti* is distributed between the 13° and 20° north latitude from southern Myanmar through central Thailand to southern Laos. *O. cuvera* is distributed between 20° and 30° north latitude from Nepal through northeastern India, northwestern Myanmar, northern Thailand, central Laos, and northern Vietnam to southern China (Mizunuma and Nagai 1994) (Fig. 1). In most of these areas, they occur allopatrically (only one of the two species is found) but in a small area of northern Thailand, they occur sympatrically (both of them are found at the same location). The color pattern on male elytra varies, especially in *O. cuvera*, at different locations, yet it never overlaps between the two species.

Table 1.   Variability and allometry of body, genitalia, and mandible length of male *O. mouhoti* and *O. cuvera* in different locations

Species & Locations	Collection spot	No. of samples	Body length		Genitalia length			Mandible length (mm)		
			Mean (mm)	CV (%)	Mean (mm)	CV (%)	Allometry*	Mean	CV (%)	Allometry*
O. mouhoti										
E. Thailand	Khao Soi Dao	31	45.1	11.9	6.59	5.2	0.32**	12.1	39.0	2.82**
C. Thailand	Khao Yai	36	46.3	12.6	6.68	5.9	0.38**	15.0	45.8	3.43**
W. Thailand	Khao Galah	32	43.8	13.8	6.28	6.9	0.37**	13.0	46.2	2.98**
N. Thailand-I	Wiangpapao	19	44.4	14.1	6.14	4.9	0.25**	13.9	46.6	3.17**
N. Thailand-II	Muangpan	19	42.6	11.6	6.17	4.1	0.29**	10.9	51.3	3.67**
Mean				12.8		5.4	0.32		45.8	3.21
CV (%)			3.14		3.88			12.17		
O. cuvera										
N. Thailand-I	Wiangpapao	15	52.2	10.5	7.63	3.7	0.23**	14.0	50.4	4.80**
N. Thailand-II	Muangpan	30	51.3	12.4	7.43	5.5	0.36**	13.7	46.5	3.22**
Assam	Darjiling	15	45.9	10.4	6.61	5.6	0.30**	14.3	46.5	4.04**
N. Vietnam	Tam Dao	31	48.3	15.4	7.09	5.2	0.26**	14.3	60.5	3.32**
Guangxi	Miaoshan	15	45.5	10.4	6.78	4.0	0.33**	13.3	49.1	3.95**
Hainan	Wuzhishan	10	47.1	12.0	6.74	3.1	0.24**	14.9	56.2	4.43**
Guangdong	Zhengbei	11	44.6	10.8	6.85	3.7	0.33**	14.6	61.8	5.75**
Sichuan	Yangyang	11	46.9	13.6	6.86	4.7	0.29**	14.1	57.9	3.61**
Hubei	Jouzhihe	16	46.3	11.8	6.77	5.1	0.36**	11.4	52.0	3.35**
Zhejiang	Kaihua	16	45.1	11.0	6.84	3.0	0.19**	13.0	49.8	3.68**
Mean				11.8		4.3	0.29		53.1	3.96
CV (%)			5.44		4.69			7.29		

* Allometric index (α) to body length.
** Regression for calculating allometric index is highly significant ($P < 0.01$).

Yellow dominates the elytra of *O. mouhoti* while black usually dominates the elytra of *O. cuvera.* This color difference is most conspicuous at their sympatric localities; thus, there is no possibility of incorrect identification of these two species.

Sample Locations. Three allopatric sites for *O. mouhoti*, eight allopatric sites for *O. cuvera*, and two sympatric sites for *O. mouhoti* and *O. cuvera* are listed in Table 1. Figure 1 shows their geographical distributions. The sampling locations covered virtually all the known geographical distributions of these species in the Asian tropics and subtropics (Mizunuma and Nagai 1994).

Collection of Specimens. I used only male individuals for this study, because they show both intra- and interspecific variation much more richly than the females. Individuals were collected on the trees and by bait (mostly fermented banana), and in light traps. Collections were conducted from 1988 to 1992 in sympatric locations and from 1985 to 2001 in allopatric locations, and included the collection of other potentially competing species. I only used locations that yielded >10 male individuals. Overall, I consider that the sample populations are representative of the natural populations at each location, because samples at all locations contained a full range of mandible polymorphism. The number of individuals taken at each location appears in Table 1.

Morphological Measurement. I measured the specimens for body length (the distance from the front of the head [excluding mandibles] to the tip of the elytra along the center line of the body), and the length of mandible in a straight line (from the base of the mandible on the head to the tip of it). I extracted the penis (the hardened chitinous structure inside the male copulating organ) from fresh or water-softened sam-

ples, and measured with a slide-caliper its straightened length to the nearest 0.1 mm under a low-magnifying microscope. I treated this as genitalia length. The color pattern on the elytra showed a great deal of variation among sites. Combining simple measurements of the widths of yellow and black bands along several horizontal lines on elytra, I estimated the proportion of yellow and black areas on the elytra of both species.

Handling of Quantitative Data. I used the Coefficient of Variation (CV; standard deviation divided by the population mean) of each character at each location in each species to describe the magnitude of intrapopulation variation. I also used the coefficient of variation of the population means of each character in each species as a measurement of interpopulation variability.

For determining the reliable range of each character mean at each location, I used a *t*-test for $P \leq 0.05$ based on the variation within each location. For determining the difference in character state between allopatry and sympatry in each species, and that between the two species in allopatry or in sympatry, I conducted analyses of variance (ANOVAs) using the mean value of each character in each location as a single value. The variation among the character values within allopatry and sympatry constituted the basis for error (Table 2).

The degree of allometry (or isometry) can be measured by $Y = aX^{\alpha}$, where X is the measurement of a basic, independent character such as body length, Y is the measurement of a dependent character whose allometric index α is to be determined, and a is a constant (Huxley 1931, Peters 1983, Labarbera 1989). I obtained allometric indices of male genitalia length and mandible length on body length through regres-

Table 2. Analyses of variance for difference between two species in allopatry and sympatry and for difference between allopatry and sympatry in two species

Difference between	In	Character	df for error	F
Allopatry and sympatry	O. mouhoti	Body length	3	1.86
		Genitalia length	3	5.32
	O. cuvera	Body length	8	37.79**
		Genitalia length	8	42.04**
O. mouhoti and O. cuvera	Allopatry	Body length	9	2.02
		Genitalia length	9	8.14*
	Sympatry	Body length	2	67.22*
		Genitalia length	2	166.84**

*, ** Statistically significantly different ($P < 0.05$, 0.01, respectively).

sion analyses; $\ln Y = \alpha \ln X + \ln a$ (natural logarithmic conversion).

Results

Confirmation of Sympatry and Allopatry. In both Wiangpapao and Muangpan (northern Thailand -I and -II), collections were conducted at several sites within an area of <10 km radius in the same mountain range. Both species were relatively rare (compared with the same species at some allopatric locations or compared with other Lucanidae species at the same location), especially *O. cuvera* at Wiangpapao and *O. mouhoti* at Muangpan, and the two species were not been collected together at the same site or in the same trap. Thus, it was not clear whether the two species shared exactly the same habitat or chose different habitats at the same location. Nevertheless, a sufficient number of samples for statistical analysis was eventually collected for both species at both locations. I treated these two locations as sympatric locations for this study.

There were some locations (e.g., Fang to the northwest of Wiangpapao) within 70 km of either Wiangpapao or Muangpan where both species were collected but without a sufficient number of specimens. I did not use these sympatric sites in the analysis. In addition, there were several localities within 100 km of either of these sympatric sites where only *O. mouhoti* was collected (e.g., Nan to the east of Muangpan). Because of their proximity to the confirmed sympatric sites, I could not altogether discard the possibility that *O. cuvera* was actually present but could not be collected at those sites. These locations were also excluded from the analysis.

In the three allopatric locations of *O. mouhoti* and eight allopatric locations of *O. cuvera* shown in Fig. 1 and Table 1, only *O. mouhoti* or *O. cuvera*, respectively, was seen over extended years of collections. This finding agrees with other records (e.g., Mizunuma and Nagai 1994). I treated these locations as allopatric locations for this study.

Other Possible Competitors. At the sympatric sites, several Lucanidae species with body size comparable to *O. mouhoti* or *O. cuvera* were also collected. They were, in order of abundance, *Dorcus titanus* (Boisduval), *Odontolabis siva* (Hope & Westwood), *D. antaeus* Hope, *D. curvidens* (Hope), *Neolucanus maximus* Houlbert, and *N. giganteus* Pouillaude. While all of the above species might compete for the same resources with *O. mouhoti* or *O. cuvera*, the ones belonging to different genera are not likely to have influenced the evolutionary interaction between *O. mouhoti* and *O. cuvera*. *O. siva* was the only congener that could be competing for the same resources. However, this species is morphologically very distinct from *O. mouhoti* or *O. cuvera*, and is therefore unlikely to have significantly affected the evolutionary interaction between *O. mouhoti* and *O. cuvera*. Furthermore, *O. siva* is found at all the sympatric and allopatric locations of *O. mouhoti* and *O. cuvera*, except for two in China (Sichuan and Hubei); consequently, competition with *O. siva*, were it ever present, would have affected populations at both allopatric and sympatric locations equally. I consider the hypothesized character displacement between *O. mouhoti* and *O. cuvera* to have been caused primarily by their own interspecific interaction.

Variability Within and Across Populations. In all populations regardless of species, variability of body length was quite high (CV = 10–15%) and variability of mandible length was invariably very high (CV = 39–60%), while genitalia length showed low variability (CV = 3–7%) (Table 1). Allometric indices of genitalia length to body length were invariably low (0.19–0.38), but those of mandible length to body length were always very high (2.82–5.75). In these analyses, the correlation coefficient between body length and mandible length (logarithmic conversion) was >0.9 in all the populations, suggesting a description with very little error of mandible allometry with body size. The correlation coefficient between body length and genitalia length (logarithmic conversion) was also highly significant in all the populations (mean of all populations, 0.81; lowest mean, 0.74**). In this situation, traditional least squares is the most appropriate method for allometry analysis (Socal and Rohlf 1995; Eberhard et al. 1999). The reliable range ($P \leq 0.05$ by t distribution) of the lowest allometric index of genitalia length was 0.19 ± 0.11 (*O. cuvera* in Zhejiang), while that of the highest was 0.38 ± 0.09 (*O. mouhoti* in Central Thailand), indicating that the low allometric indices accurately reflect the low variability of genitalia size.

In beetles, where adult morphology is fixed upon eclosion, body size reflects the environmental conditions to which each individual was exposed during the larval period. (Nutrient availability is a primary component.) Furthermore, sequential variation among adults of the same species is largely a reflection of the species' ontogenetic program (Kawano 2000, Emlen and Nihout 2001). This ontogenetic relationship, once evolved, is considered to be evolutionarily highly conservative (Emlen 1996, Kawano 1998, 2000). In male stag beetles, body measurements that are not directly influenced by sexual selection, such as elytral width, are isometric to body length; sexually selected char-
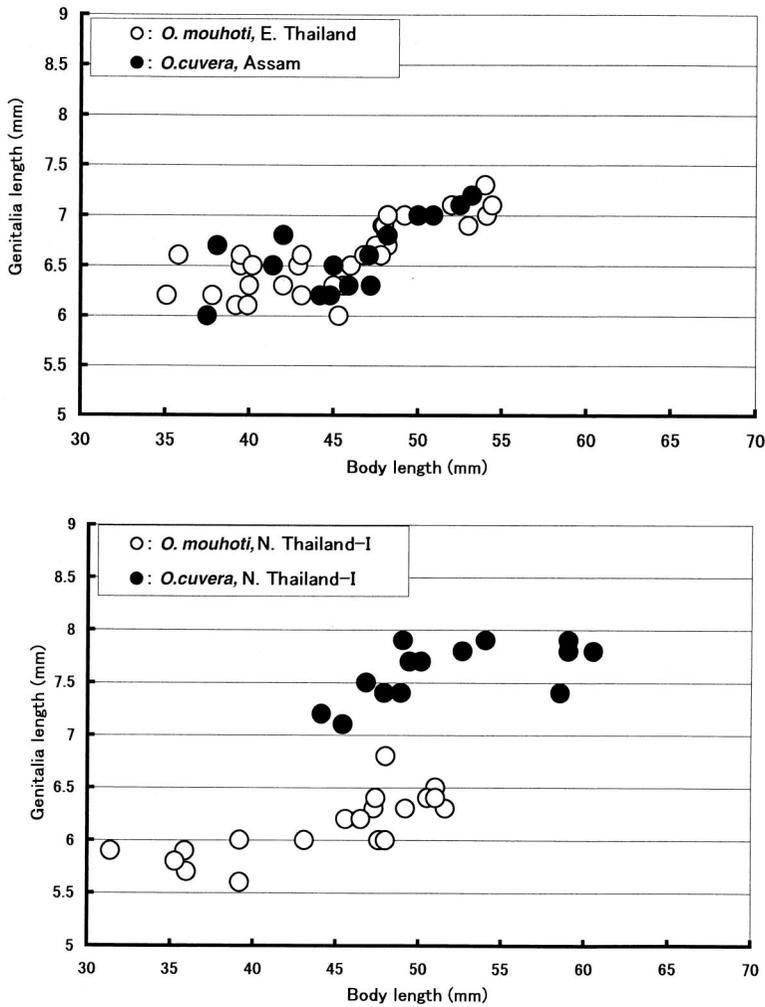
Fig. 2. Top: Relationship between body length and genitalia length of *O. mouhoti* in eastern Thailand and *O. cuvera* in Assam where each is allopatric from the other. (Note that the dimensions of the two species overlap with each other.) Bottom: Relationship between body length and genitalia length of *O. mouhoti* and *O. cuvera* at a sympatric location (northern Thailand-I). (Note that the dimensions of the two species are far apart, without any overlap.)

acters, such as mandible length, are highly positively allometric (allometric indices 2–6); and characters that are developmentally negatively affected by the development of positively allometric characters, such as hind wing length, are slightly negatively allometric to body length (allometric indices 0.7–0.9) (Kawano 1997). Thus, genitalia size clearly defies the allometric scheme of other characters and the ontogenetic relationship of genitalia with other body parts is very different from that among other body parts.

Controlled by this ontogenetic scheme, genitalia size within populations was distinctly stable compared with other morphological characters at all localities of both species. However, the variability of genitalia length across different localities (measured by the coefficient of variation of location means) was as high as that of body length (Table 1). In view of its developmentally stable nature, one can conclude that gen-

italia size is likely to be highly responsive to adaptive selection.

Morphology in Allopatry and Sympatry. When allopatric populations of *O. mouhoti* and *O. cuvera* were plotted for body length and genitalia length (e.g., *O. mouhoti* in eastern Thailand and *O. cuvera* in Assam; Fig. 2, top), the physical dimensions of the two species overlapped, suggesting that the two species might physically compete with each other. However, at the sympatric location, the two species shifted their relative sizes in opposite directions, so that the two species scarcely overlapped (e.g., in northern Thailand-I; Fig. 2, bottom).

Body Length in Allopatry and Sympatry. The mean body lengths of *O. mouhoti* at two sympatric locations tended to be smaller than those at the three allopatric locations, but the difference was short of statistical significance. In contrast, the mean body lengths of *O.*
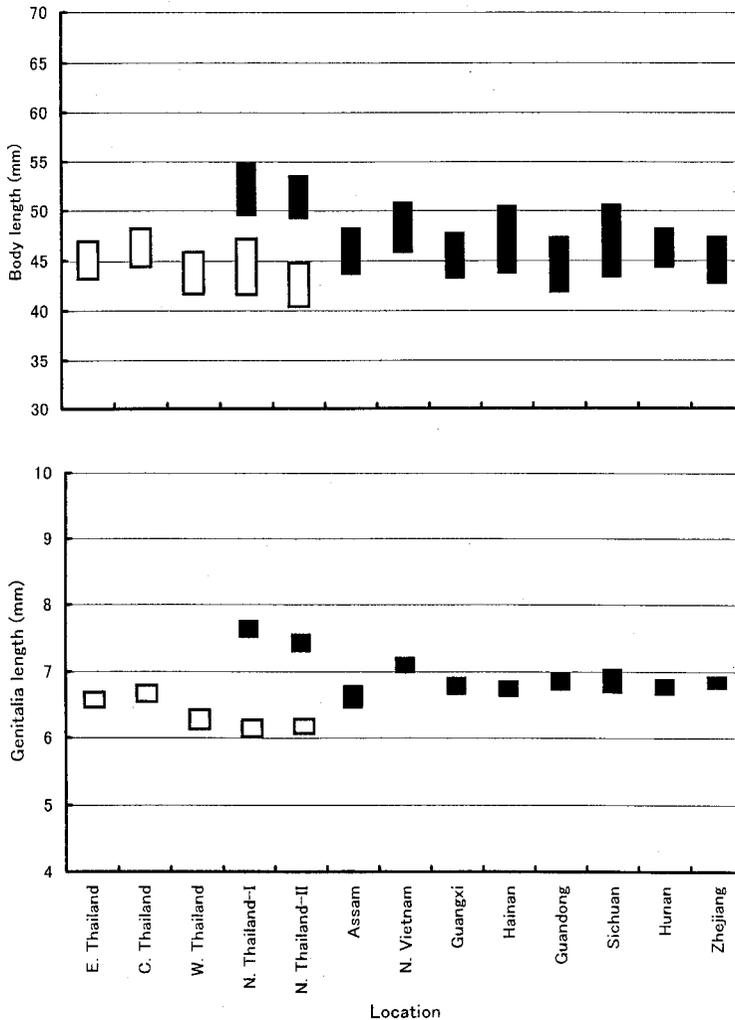
Fig. 3. Top: Body length of *O. mouhoti* and *O. cuvera* at allopatric and sympatric sites. (The 5% reliable range of mean of each population is shown by a rectangular box.) Bottom: Genitalia length of *O. mouhoti* and *O. cuvera* at allopatric and sympatric sites. (The 5% reliable range of the mean of each population is shown by a rectangular box.)

cuvera at sympatric locations were significantly greater than those at the eight allopatric locations [*t*-test, Fig. 3, top, or analysis of variance (ANOVA), Table 2]. There was no significant difference in body length between the two species at allopatric locations, but this difference was significant at sympatric locations. Consequently, the difference in body length between the two species was greater in sympatry than in allopatry (Fig. 3, top).

Genitalia Length in Allopatry and Sympatry. Mean genitalia lengths of *O. mouhoti* at two sympatric sites were significantly smaller that those at two of the three allopatric locations (Fig. 3, bottom). Mean genitalia lengths of *O. cuvera* at sympatric locations were significantly greater than those at any of the eight allopatric locations (Fig. 3, bottom). Therefore, the difference in genitalia length between the two species in sympatry was far greater than it was in allopatry. Pro-

portionally, the difference in genitalia length between the two species in sympatry was greater than the difference in body length in sympatry (22% for genitalia versus 19% for body length; proportion relative to the intrapopulation variability, 4.37 versus 1.45 mean SD).

Body Color Pattern in Allopatry and Sympatry. The color pattern on elytra was generally stable within locations for each species (Fig. 4). The elytra of *O. mouhoti* at allopatric sites were predominantly yellow, with a black area in the center occupying 5–20% of the whole elytra area (Figs. 4 and second row from top). At sympatric sites, they were overwhelmingly yellow, leaving only a thin line of black in the center (>95% yellow and <5% black, Fig. 4, bottom). The elytral color pattern of *O. cuvera* greatly differed at different allopatric locations, from predominantly yellow at Assam (60% yellow and 40% black, Fig. 4, top) to pre-
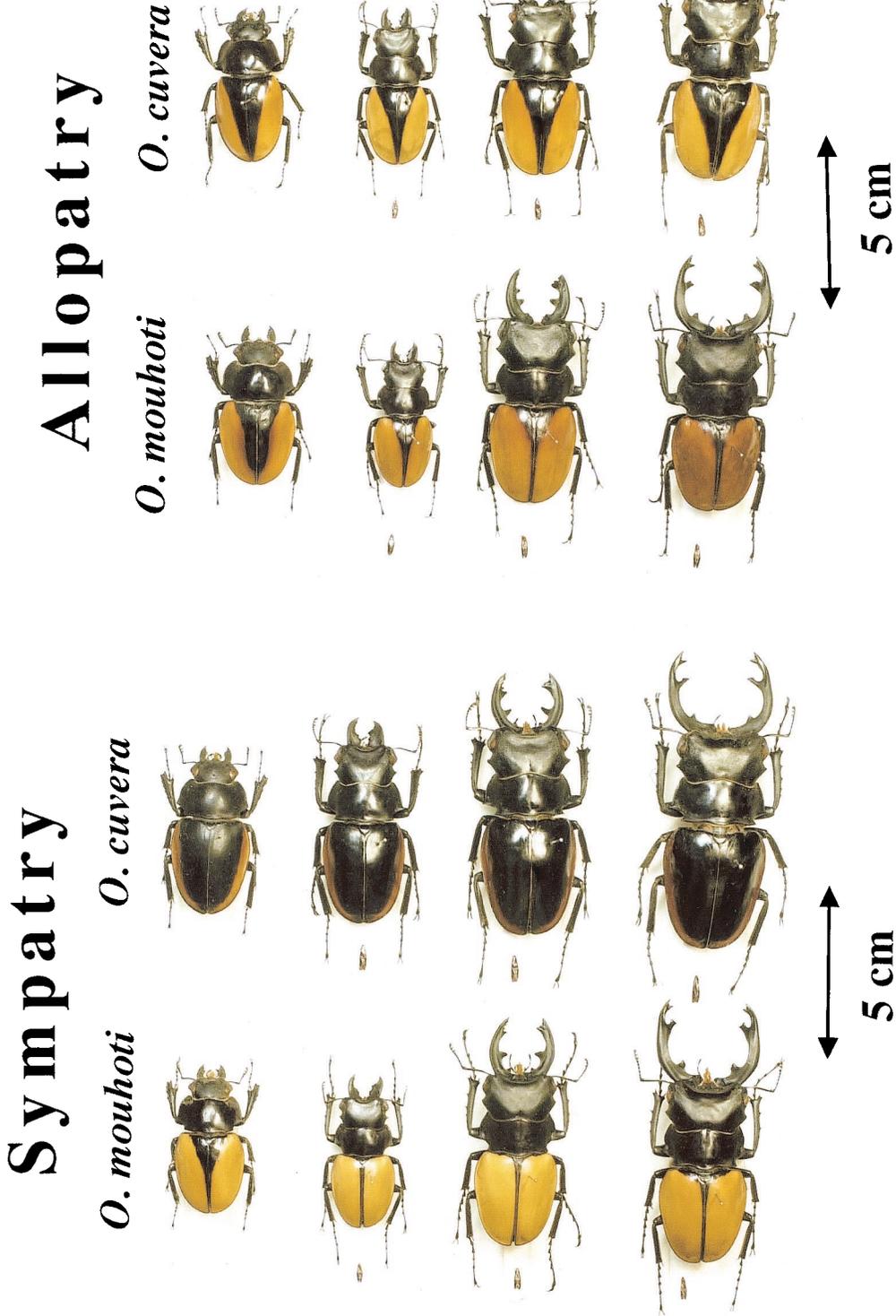
Fig. 4. Top: Male *O. cuvera* (above) and *O. mouhoti* (below) at allopatric sites (*O. cuvera* from Assam and *O. mouhoti* from eastern Thailand). Bottom: The same species at a sympatric location (northern Thailand-I). Shown are three males on the right and a female on the left, at each locality for each species. Genitalia of males are shown immediately below the body. There is a great difference between the two species in body size, genitalia length, and elytral color pattern at the sympatric site.

dominantly black at Zejiang (15% yellow and 85% black). There was no apparent correlation of the color pattern with the longitude or latitude of the collecting locality. At sympatric locations, the elytral surface was predominantly black (15% yellow and 85% black, Figs. 4 and third row from top). Thus, the color difference of elytra between the two species was most striking at sympatric locations (Fig. 4, compare lower rows to upper rows).

Discussion

This study offers an example that meets two of the three basic conditions required to confirm sympatric character displacement, i.e., character state in sympatry different from that in allopatry, and character difference in sympatry larger than that in allopatry. However, I was unable to clearly separate the allopatry/sympatry effect from other ecological effects, because (1) the number of sympatric locations is small, and (2) the distribution of allopatric locations of *O. mouhoti*, sympatric locations of both species, and allopatric locations of *O. cuvera* roughly follow a south-north gradient rather than a random distribution. Assuming that body and genitalia sizes of both species decrease from south to the north, it is possible that the large difference in body and genitalia sizes between the two species in northern Thailand exists because the size of *O. mouhoti* is smallest at the northern end of its distribution (sympatric locations in northern Thailand), while that of *O. cuvera* is largest at the southern end of its distribution (sympatric locations in northern Thailand). Color pattern differences between the two species, which are most enhanced in sympatry but not obviously correlated with latitude, strongly suggest character displacement caused by interspecific interaction. However, some uncertainty remains here also, because of the relatively small number of sample locations. More cases of sympatric species interaction would strengthen these conclusions.

The fact that sympatric character displacement is largest for genitalia size suggests that existing species maintain themselves as integrated units by enhancing reproductive isolation. In most beetle species, including stag beetles, the male mounts the female from behind during copulation, locking her underneath and thrusting the penis toward the tip of the female's abdomen. The penis, through which the sperm is injected into the female's body, bridges the gap between the copulating insects. Thus, the physical length of genitalia may be important for mating success. In *Chalcosoma* beetles, the penis is 22–35% of the body length and the difference in penis length between competing species in sympatry is 24% of the mean penis length of competing species; thus, it is highly likely that the difference in penis length has a reproductive isolating effect in those species (Kawano 2002). In the stag beetles in this study, penis length is only 12–18% of body length, and the difference in penis length between *O. mouhoti* and *O. cuvera* in sympatry is 20% of the mean of the two species, making differences in

penis length less plausible as reproductive isolating mechanisms. However, during copulation in stag beetles, the cylindrical organ covering the penis first protrudes from the body, and then the penis protrudes further from it to engage the female vagina. This suggests that in stag beetles the penis bridges only half the distance between the male and female bodies. The effective length of this bridging organ in *Odontolabis* beetles may be 24–36% of the body length and the difference in effective penis length between competing species in sympatry remains 20% of the mean effective penis length. It is interesting to note that these percentages are virtually identical in both rhinoceros beetles and stag beetles. It is therefore possible that penis length functions as a physical factor for reproductive isolation in stag beetles as well.

Most stag beetle species, including *Odontolabis*, spend their larval period feeding on decayed trees, whereas adults feed on tree saps and mate on the same tree (Suzuki 2000, Nishiyama 2000). Males of the same species are commonly seen fighting with each other to secure a female. Additional observations, such as whether competition actually occurs and differences in character state actually relate to differences in resource use, are needed to determine whether the presently observed character displacement is genetic or nongenetic, as well as whether it is ecological (avoiding competition) or reproductive (minimizing the possibility of hybridization). The fact that the degree of character displacement is greater in genitalia size and that genitalia size is very stable within populations strongly suggest that character displacement has a genetic rather than a nongenetic cause (Kawano 2002). This conclusion also suggests that the present case has more to do with strengthening reproductive isolation. Stronger displacement in genitalia size both in *Chalcosoma* and *Odontolabis* suggests that reproductive character displacement may be widespread among sexually dimorphic beetles. It is beyond the scope of this article to identify the actual mechanism of character displacement. With a comprehensive hybridization experiment we could investigate this more fundamental problem.

As to how these species have come to the present status, the most orthodox interpretation is that they evolved allopatrically and, by range expansion, came into secondary contact at sympatric locations through morphological displacement and behavioral evolution. Under this scenario, character displacement is a result of competition between existing species (classical reinforcement).

The second scenario starts from sympatric divergence. With geographic spread of the resulting differentiated populations, some locations remained sympatric but many additional allopatric populations were established. Under this scenario, divergent or disruptive selection completes the process of speciation; the two species are the result, not the cause, of character displacement (Schluter 1994, 1996, Orr and Smith 1998). Whether the origin of these two species followed the first or the second scenario, the present

results suggest that each species currently behaves as an integrated, reproductively isolated unit.

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