

Character Displacement in Giant Rhinoceros Beetles

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ABSTRACT: I quantitatively analyzed male morphology of two closely related rhinoceros beetles species (*Chalcosoma caucasus* F. and *Chalcosoma atlas* L.) in 12 allopatric and seven sympatric locations throughout Southeast Asia. The qualitative features and the magnitude of intraspecific variation of each species were unaltered between allopatric and sympatric locations. Across allopatric locations, body size, horn size, dimorphic dimension, and genitalia size nearly completely overlapped between *C. caucasus* and *C. atlas*. Yet, in all sympatric locations, the differences between the two species in these characters were highly significant. While the enlarged difference between the two species in body size in sympatry could be attributed to habitat differentiation, that in genitalia size far exceeded what was expected from the general body-size displacement. These results indicate that morphological character displacement in sympatry was most complete in sexual organs. This may account for the process of existing species conserving themselves as integrated units by avoiding interspecific competition and enhancing reproductive isolation.

Keywords: character displacement, sympatry, allopatry, rhinoceros beetles, genitalia size, body size.

Since Darwin's time, the effects of interspecific interaction, or competition, on the phenotypes and genotypes of given species has been an important topic in evolutionary biology. This is particularly interesting when the interacting species are phylogenetically close to each other and their habitats are overlapping or in close contact (Schoener 1982). There has been considerable discussion of how one interacting species dominates the other species in a common habitat (e.g., Roughgarden 1983) and 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 adapted to different conditions within the same area. It is also assumed that two species competing for the same resources can coexist if the com-

petition between the two species is less intensive than the intraspecific competition (Futuyma 1986).

It is frequently observed that when closely related species occur in microsympatry, they are subtly different from each other in the exact location of habitat, such as elevation (e.g., Diamond 1970), or in external morphology, such as the beaks of birds (e.g., Lack 1947) or the mandibles of beetles (e.g., Hori 1982). 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 the habitat use of one species differs from that of a competing species when the two species are in sympatry (interacting with one another) but overlaps when they are in allopatry (not interacting with one another), the difference is considered to have been caused by interspecific interaction (e.g., in salamanders [Hairston 1951] and New Guinean birds [Diamond 1970]). This habitat differentiation 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). Some examples such as Darwin's finches in the Galápagos archipelago (Lack 1947; Abbott et al. 1977; Grant and Grant 1982; Schluter and Grant 1984) or shells in a Danish fjord (Fenchel and Christiansen 1977) are presumably the cases of character displacement as a result of interspecific interaction.

However, establishing unambiguously that the character state of one population in sympatry is influenced by the presence of a coexisting, ecologically similar species is not easy (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 a population (Schoener 1982). Thus, to establish that a shift in character state is the result of competitive character displacement, the component of variation solely attributable to sympatry has to be clearly

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Table 1: Sampling locations and numbers of individuals in each morph in each *Chalcosoma* species

| Location | Collection spot | Allopatric or sympatric | Number of individuals sampled | | | | | |
|------------------|------------------|-------------------------------|-------------------------------|-------|-------|-----------------|-------|-------|
| | | | <i>C. caucasus</i> | | | <i>C. atlas</i> | | |
| | | | Total | Major | Minor | Total | Major | Minor |
| West Java | Puncak-Cibodas | Allopatric | 76 | 28 | 48 | | | |
| Central Java | Mt. Slamet | Allopatric | 13 | 3 | 10 | | | |
| East Java | Mt. Simerut | Allopatric | 20 | 10 | 10 | | | |
| Lampung | Mt. Tebak | Sympatric | 39 | 12 | 27 | 29 | 19 | 10 |
| South Sumatra | Mt. Dempo | Sympatric | 37 | 15 | 22 | 27 | 15 | 12 |
| Kerinci | Mt. Kerinci | Sympatric | 29 | 11 | 18 | 25 | 11 | 13 |
| West Sumatra | Minang Highland | Sympatric | 81 | 29 | 52 | 57 | 29 | 28 |
| Nias | Nias Island | Sympatric | 14 | 4 | 10 | 59 | 17 | 42 |
| Central Malay | Cameron Highland | Sympatric | 47 | 19 | 28 | 34 | 13 | 21 |
| East Thailand | Khao Soi Dao | Sympatric | 34 | 11 | 23 | 36 | 14 | 22 |
| Central Thailand | Khao Yai | Allopatric | | | | 91 | 49 | 42 |
| West Thailand | Khao Galah | Allopatric | | | | 16 | 7 | 9 |
| East Laos | Lak Sao | Allopatric | | | | 25 | 6 | 19 |
| Central Sulawesi | Sampuraga Pass | Allopatric | | | | 28 | 18 | 10 |
| North Sulawesi | Manado | Allopatric | | | | 20 | 11 | 9 |
| Leyte | Leyte Island | Allopatric | | | | 53 | 22 | 31 |
| East Mindanao | Mt. Apo | Allopatric | | | | 29 | 17 | 12 |
| Central Mindanao | Mt. Nibo | Allopatric | | | | 39 | 12 | 27 |
| West Mindanao | Zamboanga | Allopatric | | | | 35 | 12 | 23 |

separated from the variation attributable to other causes, such as differences in the habitat conditions of allopatric and sympatric locations (Dunham et al. 1979; Waage 1979; Connor and Siberloff 1986).

Two giant rhinoceros beetle species in the genus *Chalcosoma* (*Chalcosoma caucasus* F. and *Chalcosoma atlas* L.) are widely distributed in tropical Asia and are among the largest beetles in Asia. The genus *Chalcosoma* contains only these two species and a more narrowly distributed *Chalcosoma moellenkampi* Kolbe, and no other genus is morphologically similar to this genus. Thus, *Chalcosoma* stands as one of the most conspicuous and unique groups of insects. Darwin (1874, pp. 327–328) once remarked “If we could imagine a male *Chalcosoma* with its polished bronzed coat of mail, and its vast complex horns, magnified to the size of a horse, or even of a dog, it would be one of the most imposing animals in the world.” While in many locations only one species is found, there are several locations where both species are found. These species 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, extreme allometric variation of horns, and marked dimorphism are the main features. The male dimorphism is composed of a minor morph with smaller body, shorter horns, and comparatively large wings and a major morph with larger body, disproportionally long horns, and comparatively small wings (Kawano 1991, 1995a).

Male dimorphisms are known to be common in beetle species with fighting apparatus such as in rhinoceros beetles (Eberhard 1979, 1980, 1982; Eberhard and Gutierrez 1991; Kawano 1991, 1995a), stag beetles (Kawano 1989, 1992), and dung beetles (Cook 1987; Emlen 1994). Male morphological dimorphism has been often considered to be related to male alternative behaviors for finding or securing females for mating (Eberhard 1980, 1982; Cook 1987; Siva-Jothy 1987; Kawano 1991, 1992).

In preliminary studies (Kawano 1993, 1995b, 1997), I found body-size displacement at a few sympatric locations. In this study, I analyzed the male body size, horn length, dimorphic configuration, and, more importantly with respect to reproductive isolation as a possible cause of sympatric character displacement, the male genitalia size of the two *Chalcosoma* species using large population samples in 12 allopatric and seven sympatric locations throughout Southeast Asia. I tried to establish the case of sympatric character displacement beyond any statistical doubt and describe the biological nature of species interaction.

Material and Methods

Species Studied

Chalcosoma caucasus F. is the largest rhinoceros beetle and one of the largest insects in Asia. It is distributed from Java to East Thailand and seen in the medium elevation

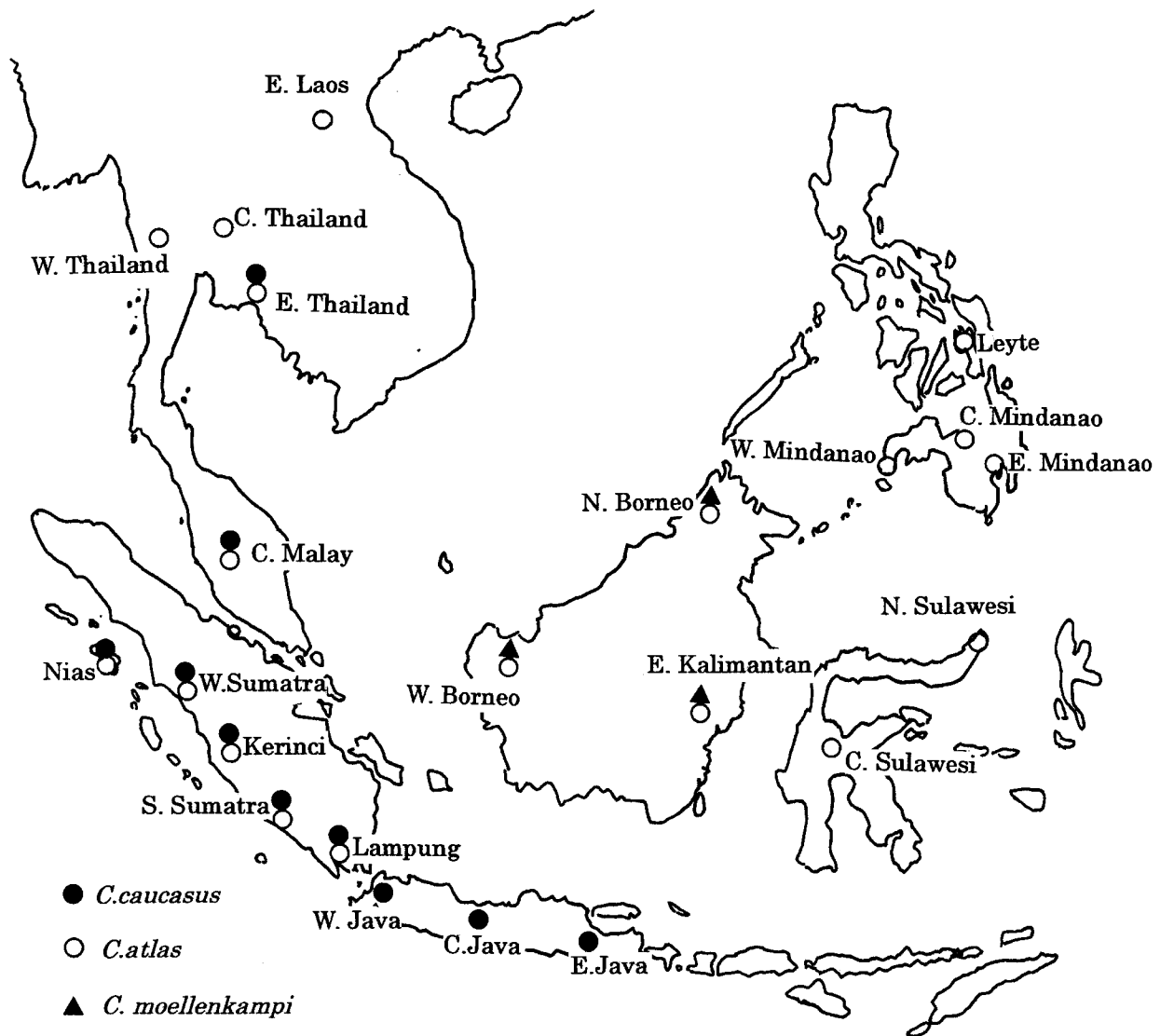


Figure 1: Geographic distribution of allopatric and sympatric locations of *Chalcosoma caucasus* and *Chalcosoma atlas*, where samplings for this study were successful. Sympatric locations of *Chalcosoma moellenkampii* and *C. atlas* are also shown.

forests (mainly 800–1,500 m a.s.l.). *Chalcosoma atlas* L. is on average smaller (by some 16% in body length in overall location mean) than *C. caucasus*. It is found in the low- to medium-elevation forests (mainly 0–1,200 m a.s.l.) throughout Southeast Asia except Java (Unno 1993). There is a third species of *Chalcosoma*, *Chalcosoma moellenkampii* Kolbe, endemic to Borneo, which is sympatric with *C. atlas*. However, no allopatric populations of *C. moellenkampii* were available, so I did not include it in this study, nor did I include *C. atlas* from Borneo.

Identification of Species

Individuals observed in this study could be identified by the following features. In medium to large male individuals, a conspicuous tooth on the lower side of the head horn easily distinguishes *C. caucasus* from *C. atlas*. In small males, a stick-shaped head horn distinguishes *C. caucasus* from *C. atlas*, which has a spoon-shaped head horn (Hisamatsu 1982; Unno 1993; Mizunuma 1999). The thorax horns of *C. caucasus* are distinctly smaller (none at all in

Table 2: Difference in body, head horn, and genitalia length (mm) of *Chalcosoma caucasus* (*C.c.*) and *Chalcosoma atlas* (*C.a.*) in allopatry compared with that in sympatry

| Character | Allopatry | | | Sympatry | | | All | | $(S - A)/M$ (%) | S/A |
|-------------------|-------------|-------------|----------------------------------|-------------|-------------|----------------------------------|--|---------------------|--------------------|---------|
| | <i>C.c.</i> | <i>C.a.</i> | <i>C.c.</i> - <i>C.a.</i> (A) | <i>C.c.</i> | <i>C.a.</i> | <i>C.c.</i> - <i>C.a.</i> (S) | <i>C.c.</i> + <i>C.a.</i> (mean, <i>M</i>) | <i>S</i> - <i>A</i> | | |
| Body length: | | | | | | | | | | |
| All individuals | 66.3 | 60.8 | 5.5 | 70.4 | 55.2 | 15.2 | 62.7 | 9.7 | 15.5 | 2.8 |
| Major morph only | 71.8 | 65.0 | 6.8 | 74.8 | 59.1 | 15.7 | 66.9 | 8.9 | 13.3 | 2.3 |
| Minor morph only | 63.3 | 56.6 | 6.7 | 68.0 | 51.3 | 16.7 | 59.0 | 10.0 | 16.9 | 2.5 |
| Head horn length: | | | | | | | | | | |
| All individuals | 27.1 | 24.4 | 2.7 | 28.6 | 21.4 | 7.2 | 25.0 | 4.5 | 18.0 | 2.7 |
| Major morph only | 42.3 | 34.6 | 7.7 | 44.6 | 31.0 | 13.6 | 37.2 | 5.9 | 15.9 | 1.8 |
| Minor morph only | 18.5 | 15.4 | 3.1 | 19.7 | 12.9 | 6.8 | 16.1 | 3.7 | 23.0 | 2.2 |
| Genitalia length: | | | | | | | | | | |
| All individuals | 13.6 | 13.8 | -.2 | 15.2 | 12.1 | 3.1 | 13.7 | 3.3 | 24.1 | (-)15.5 |
| Major morph only | 14.0 | 14.3 | -.3 | 15.5 | 12.4 | 3.1 | 14.1 | 3.4 | 24.1 | (-)10.3 |
| Minor morph only | 13.4 | 13.3 | .1 | 15.0 | 11.8 | 3.2 | 13.4 | 3.1 | 22.5 | 31.0 |

the smallest individuals) than those of *C. atlas* of the same body size. Regardless of the size, *C. caucasus* males have larger and more conspicuous stipples on both sides of the thorax than *C. atlas* (Mizunuma 1999).

Quantitative characters such as body length of the two species greatly differed among locations; yet, the qualitative traits representing the species stayed unchanged throughout all the locations, allopatric and sympatric. Thus, there was no difficulty in identifying the two species in any location. In addition to the 992 male individuals used in this study, I have observed more than 1,500 male individuals of *C. caucasus* and *C. atlas*, and I could identify all the individuals readily into either of the two species. Thus, these species could be considered as a typical "good species" in morphological taxonomy.

Sample Locations

Three allopatric locations for *C. caucasus*, nine allopatric locations for *C. atlas*, and seven sympatric locations for *C. caucasus* and *C. atlas* are listed in table 1. Figure 1 shows their geographical distribution. The sampling locations covered virtually all Southeast Asia.

Collection of Sample Individuals

I used only male individuals for this study because they show both intra- and interspecific variation much more richly than do females. Sample individuals were collected mainly by light traps. There was some tendency for the proportions of small males and females to be higher when the traps were set at the peripheral sides of the habitat and at the early periods of adult emergence. Nevertheless, even the samples caught at the center of the collection

area in the middle of adult emergence period always included a significant proportion of small males. Overall, I consider that the sample populations used in this study are good representations of the natural population in the location. The actual collections were conducted from 1985 to 2000. The numbers of individual samples in each location appear in table 1.

Morphological Measurement

I measured the samples for body length (the distance from the front of the head [excluding horn] to the tip of the elytra along the center line of the body) and the length of head horn in a straight line (from the base of the horn on the head to the tip of the horn). I extracted the male copulating organ (penis; the part chitinously hardened) from fresh or water-softened samples and measured the length of the straightened penis under a low-magnifying microscope with a slide caliper to the nearest 0.1 mm. I treated this as genitalia length.

Detection of Dimorphism

Two-dimensional plotting of each sample for body length and head horn yielded two readily recognizable morphs in most populations. In a few cases, some samples did not fall into either of the two morphs in a clear-cut manner. Head horn of all the individuals falling clearly in the major morph had a straight tip, while the majority of minor morph individuals had a tooth spreading in a wide angle on the tip of the horn in both species. Thus, I included those intermediate individuals with a straight tip in the major morph and those with spreading tooth in minor morph.

Table 3: ANOVA for the difference between allopatric and sympatric locations

| Species and character | df for error | F value |
|-------------------------------------|--------------|---------|
| <i>Chalcosoma caucasus:</i> | | |
| Body length: | | |
| All individuals | 8 | 43.31** |
| Major morph only | 8 | 7.10* |
| Minor morph only | 8 | 38.89** |
| Head horn length: | | |
| All individuals | 8 | .95 |
| Major morph only | 8 | 3.18 |
| Minor morph only | 8 | .39 |
| Genitalia length: | | |
| All individuals | 8 | 46.26** |
| Major morph only | 8 | 34.36** |
| Minor morph only | 8 | 50.40** |
| <i>Chalcosoma atlas:</i> | | |
| Body length: | | |
| All individuals | 14 | 88.8** |
| Major morph only | 14 | 38.59** |
| Minor morph only | 14 | 15.46** |
| Head horn length: | | |
| All individuals | 14 | 5.64* |
| Major morph only | 14 | 9.29** |
| Minor morph only | 14 | 9.36** |
| Genitalia length: | | |
| All individuals | 14 | 31.17** |
| Major morph only | 14 | 52.59** |
| Minor morph only | 14 | 15.20** |
| <i>C. caucasus:</i> | | |
| Coefficient of variation in length: | | |
| Body length | 8 | .01 |
| Head horn length | 8 | 0 |
| Genitalia length | 8 | .37 |
| <i>C. atlas:</i> | | |
| Coefficient of variation in length: | | |
| Body length | 14 | .03 |
| Head horn length | 14 | 1.79 |
| Genitalia length | 14 | 4.88* |

* Statistically significant difference at .05.

** Statistically significant difference at .01.

Quantification of Intraspecific Variability

I used the coefficient of variation (CV; SD divided by the population mean) for describing the magnitude of intraspecific variation in each character in each location in each species. Body length and genitalia length could be considered as following a normal distribution; thus, the CV could appropriately represent the corresponding intraspecific variability. However, head horn length showed a bimodal distribution due to its dimorphic divergence; thus, the CV represented a combination of intraspecific dimorphism and the variability within each morph in each species.

Measurement of Sympatric Effect

In most comparisons in allopatry and in all the comparisons in sympatry, the body, head horn, and genitalia lengths of *C. caucasus* were greater than those of *C. atlas*. I first obtained $(C.c. - C.a. \text{ in sympatry}) - (C.c. - C.a. \text{ in allopatry})$, where *C.c.* and *C.a.* are the character states (mean of all locations in each patry) of *C. caucasus* and *C. atlas*, respectively. The proportion of this value to the whole population (both species) mean measures the relative magnitude of sympatric effect in each character. The ratio $(C.c. - C.a. \text{ in sympatry}) / (C.c. - C.a. \text{ in allopatry})$ measures the difference in sympatry relative to that in allopatry in each character (table 2).

Statistical Analyses

For determining the reliable range of each character mean at each location, I used a *t*-test for 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 across

Table 4: ANOVA for the difference between *Chalcosoma caucasus* and *Chalcosoma atlas* in allopatry and sympatry

| Comparison and character | df for error | F value |
|------------------------------|--------------|----------|
| Difference across allopatry: | | |
| Body length: | | |
| All individuals | 10 | 55.68** |
| Major morph only | 10 | 27.46** |
| Minor morph only | 10 | 28.98** |
| Head horn length: | | |
| All individuals | 10 | 3.09 |
| Major morph only | 10 | 39.26** |
| Minor morph only | 10 | 7.29* |
| Genitalia length: | | |
| All individuals | 10 | .22 |
| Major morph only | 10 | .51 |
| Minor morph only | 10 | .04 |
| Difference in sympatry: | | |
| Body length: | | |
| All individuals | 12 | 661.59** |
| Major morph only | 12 | 486.46** |
| Minor morph only | 12 | 474.90** |
| Head horn length: | | |
| All individuals | 12 | 28.26** |
| Major morph only | 12 | 145.80** |
| Minor morph only | 12 | 28.69** |
| Genitalia length: | | |
| All individuals | 12 | 290.67** |
| Major morph only | 12 | 257.85** |
| Minor morph only | 12 | 264.19** |

* Statistically significant difference at .05.

** Statistically significant difference at .01.

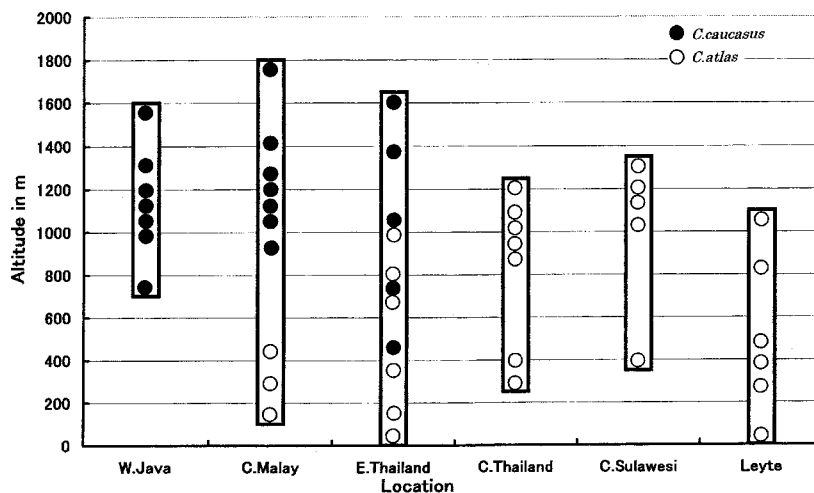


Figure 2: Altitudinal distribution of *Chalcosoma caucasus* and *Chalcosoma atlas* in allopatric and sympatric locations

allopatry or in sympatry, I conducted 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 (tables 3, 4).

To determine the effect of allopatry/sympatry on the relationship of body size with horn and genitalia sizes, I conducted a series of hierarchical covariance analyses in which body length was the independent variable and head horn or genitalia length was the dependent variable, and allopatry/sympatry and location (within each patry) were the source of influence to the regression of dependent character on body length. In a covariance analysis of head horn length (H) on body length (L) in allopatric and sympatric locations in one species, for example, the total variance of H is composed of variance components attributable to total regression, allopatry/sympatry effect on regression, location (within each patry) effect on regression, and unaccountable variation. Thus, the total variance in H can be partitioned into separate components. The deviation from regression in each location in each patry was regarded as unaccountable variation that I used as the error variance for the statistical test. The allopatry/sympatry effect can be further split into effects corresponding to different heights (intercept) of regression and different regression coefficients (slope) by subtracting the variance corresponding to the deviation from the common regression, where the regressions in allopatry and sympatry are adjusted to the same height. The same treatment can be applied to location effect within patry. I gave a detailed description of this procedure in a previous article (Kawano 2000).

Results

Confirmation of Sympatry and Allopatry

In each sympatric location, collections were conducted at several sites within an area of <10 km radius in the same mountain range. In West Sumatra, collections came from four sites (near Padangpanjang, Payakumbuh, Solok, and Padang; 25–40 km from each other) within an area of 60 km radius in and around Minang Highland. These sites can be considered as parts of the same mountain range, and each site yielded samples of both *Chalcosoma caucasus* and *Chalcosoma atlas*, each with major and minor morphs. There was no statistically significant difference in morphological measurements among the four male populations coming from the four collection sites in each species. Thus, I lumped all the collected samples from these sites together to be treated as one population representing West Sumatra. In all these locations, both *C. caucasus* and *C. atlas* could eventually be collected in good numbers without an extreme rarity of either species, except in Nias, where *C. caucasus* was much less abundant than *C. atlas*.

Although *C. caucasus* was nearly always found at higher and *C. atlas* at lower elevations at sympatric locations, individuals of both species were attracted to the same light trap at a single point in several sympatric locations. Seven sympatric locations of *C. caucasus* and *C. atlas* are shown in figure 1 and listed in table 1.

In the nine allopatric locations of *C. atlas* shown in figure 1 and table 1, only *C. atlas* were seen. This agreed with other reports (e.g., Unno 1993) that no other *Chalcosoma* species were distributed in these locations. My observations over more than 10 yr support this view.

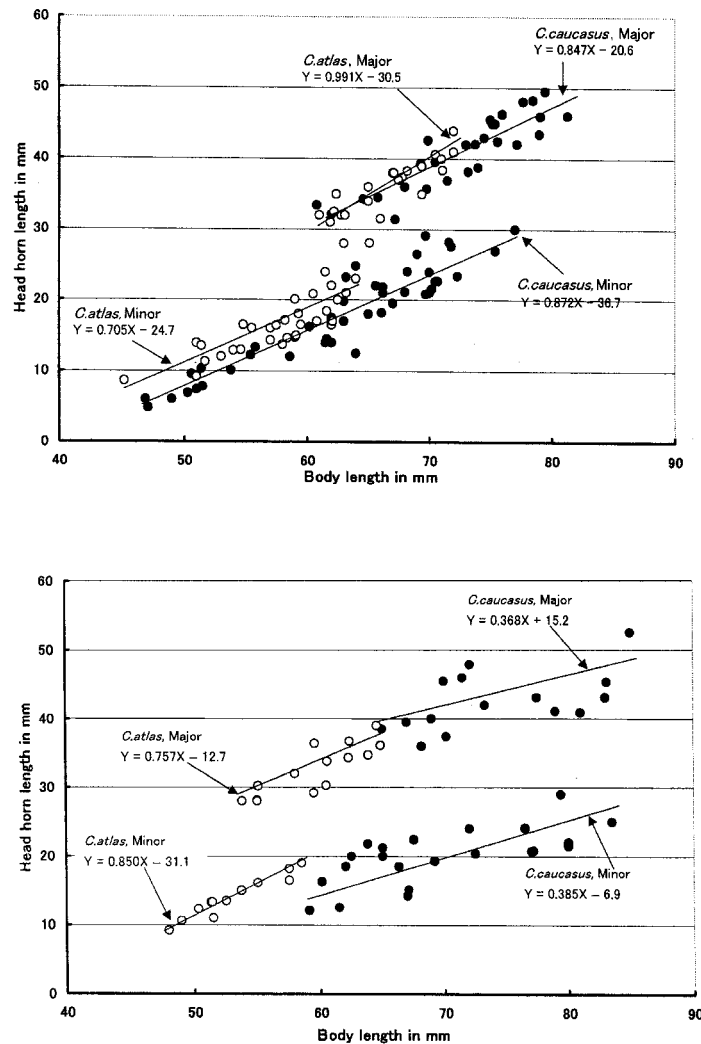


Figure 3: Top, relationship between body length and head horn length in *Chalcosoma caucasus* in West Java and *Chalcosoma atlas* in Leyte, where each is allopatric from the other. Note that the morphological dimensions of the two species overlap. Bottom, relationship between body length and head horn length in *C. caucasus* and *C. atlas* in a sympatric location (South Sumatra). Note that the morphological dimensions of the two species hardly overlap.

Some popular books (e.g., Unno 1993) describe both *C. caucasus* and *C. atlas* from Java. Aside from the 76 sample individuals I collected in the area along Puncak and Cibodas, West Java, I inspected >1,000 individuals collected over an area of >35 km radius, including Mount Salak, Mount Gede, and Mount Pangolango, West Java, and all were *C. caucasus*. In the low elevation areas with the radius of up to 50 km surrounding the above area, I could not find any other record of *Chalcosoma* species. In addition to the 13 *C. caucasus* individuals from Central Java and the 20 from East Java that I used in this study, I inspected a considerable number of specimens in other private collections that were all *C. caucasus*. I also inspected

several specimens kept at public insectariums in East Java that were labeled as *C. atlas*; however, they were all *C. caucasus*. I could not find any trace of *C. atlas* from Java in more than 10 yr of observations. Thus, I judged West, Central, and East Java to be allopatric locations of *C. caucasus*.

Altitudinal Distribution in Allopatric and Sympatric Locations

Figure 2 presents the altitude at six collection locations where accurate altitudes were available. From these data,

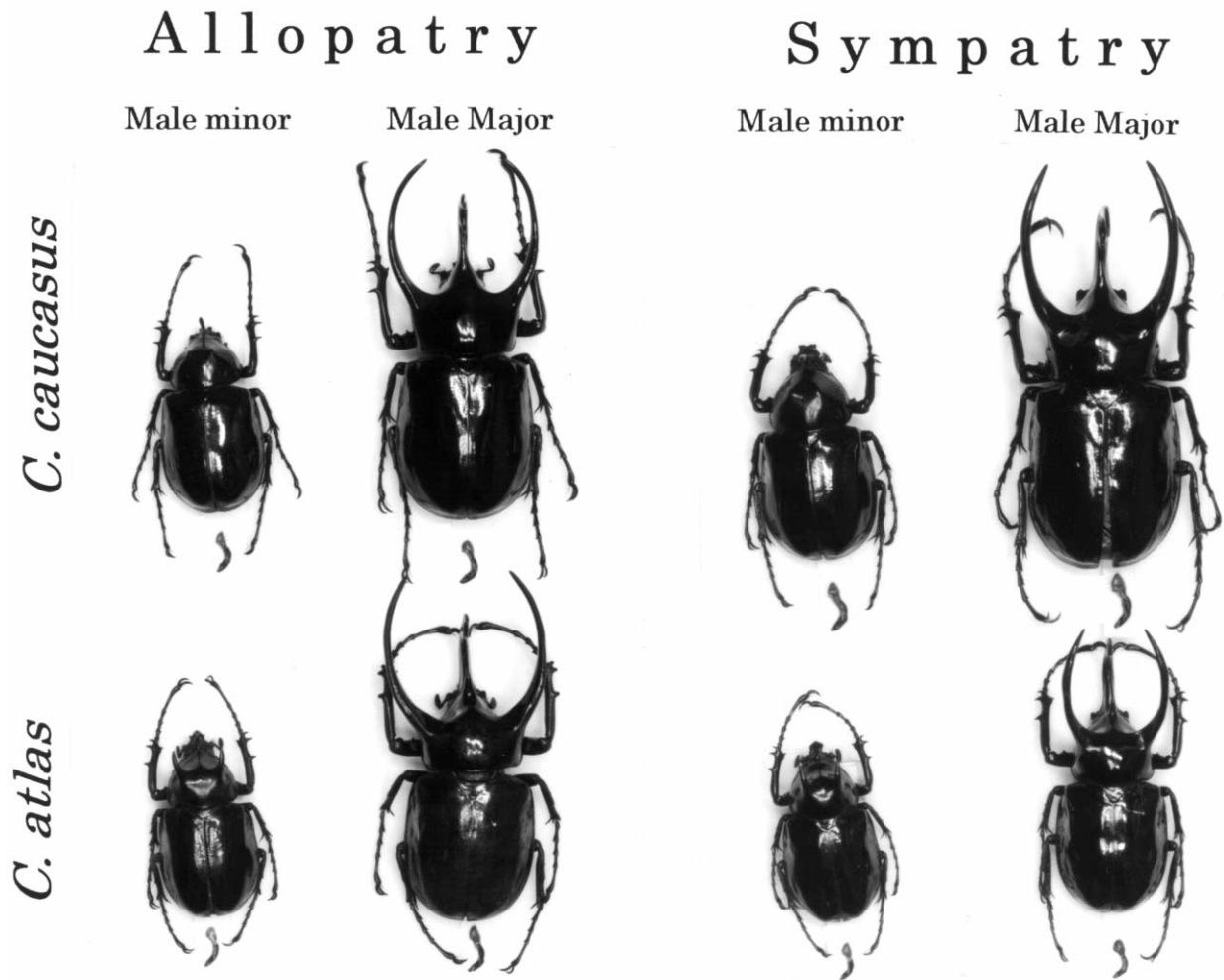


Figure 4: Male *Chalcosoma caucasus* (top) and *Chalcosoma atlas* (bottom) in allopatric locations (*C. caucasus* from West Java and *C. atlas* from Leyte; left) and in a sympatric location (South Sumatra; right). Major morph on the right and minor morph on the left side in each location in each species. There is a great difference between the two species, both in body size and genitalia length in the sympatric location. Side view of genitalia from each sample is shown immediately below the body.

I extrapolated possible altitudinal distributions of the two species.

Detection of Dimorphism

All the male populations of the two species showed a divergence into two morphs, that is, a minor morph with comparatively small body and short horns and a major morph with larger body and disproportionally larger horns (figs. 3, 4). Only in Kerinci and Central Malay (*C. caucasus*), East Thailand (both species), and Leyte (*C. atlas*), were there some individuals (1–3 per location) that could not be readily judged to belong to either morph (<1% of the total of 992 males). These intermediate individuals

were included in either of the two morphs following the criteria described earlier. In all other populations of the three species, all the sampled individuals were clearly assignable to one of the two morphs.

Morphology in Allopatry and Sympatry

When allopatric populations of *C. caucasus* and *C. atlas* were plotted for body length and horn length (e.g., *C. caucasus* in West Java and *C. atlas* in Leyte; fig. 3, top), the physical dimensions of the two species overlapped within each morph, suggesting that the major morphs of the two species might be in direct conflict with each other; the same was true for the minor morphs. However, in all

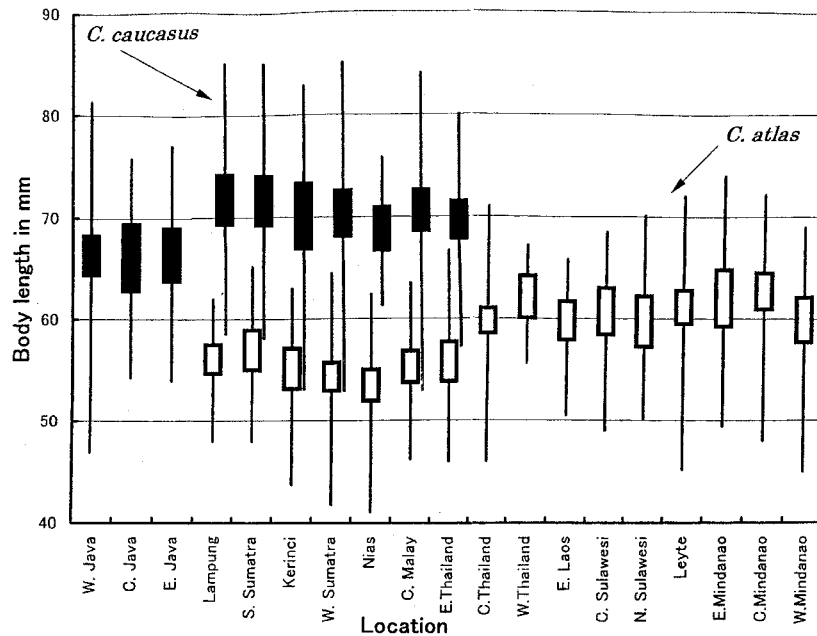


Figure 5: Body length of *Chalcosoma caucasus* and *Chalcosoma atlas* in allopatric and sympatric locations. The 5% reliable range of mean of each population is shown by a rectangular box, and the maximum and minimum values are shown by a vertical line.

the sympatric locations, major morphs of the two species shifted their relative size in opposite directions, as did the minor morphs, so that within each morph, the two species scarcely overlapped (e.g., in South Sumatra; fig. 3, *bottom*).

Body Length in Allopatric and Sympatric Locations

The mean body lengths of male *C. caucasus* in all seven sympatric locations were greater than those in the three allopatric locations, and mean body lengths of *C. atlas* in all seven sympatric locations were, on the contrary, highly significantly smaller than those in the nine allopatric locations (fig. 5). Similar comparisons within morphs showed the same pattern. The major and minor morphs of *C. caucasus* at the sympatric locations were larger than those of corresponding morphs at the allopatric locations, and the major and minor morphs of *C. atlas* at the sympatric locations were smaller than the corresponding morphs at the allopatric locations. Statistical analyses by *t*-test (fig. 5) or ANOVA (table 3) support this conclusion. Accordingly, the difference in body size between the two species in sympatry was distinctly greater than that in their corresponding allopatric locations.

Genitalia Length in Allopatric and Sympatric Locations

When allopatric populations of the two species were plotted for body length and genitalia length, the dimensions of the two species nearly completely overlapped (e.g., *C. caucasus* in West Java and *C. atlas* in Leyte; fig. 6, *top*). However, in all the sympatric locations, the genitalia of *C. caucasus* were distinctly larger than those of *C. atlas* (fig. 7), and the body length/genitalia length dimensions of the two species never overlapped (e.g., in South Sumatra; fig. 6, *bottom*). Accordingly, the genitalia of *C. caucasus* in sympatric locations were highly significantly larger than those in allopatric locations, and the genitalia of *C. atlas* in sympatric locations were, on the contrary, highly significantly smaller than those in allopatric locations (fig. 7; table 3).

While the differences in mean body length and mean head horn length between the two species in sympatric locations were highly significant (table 4), there was considerable overlap between individuals of the two species (fig. 5). Large-body *C. atlas* were larger than small-body *C. caucasus* in all the sympatric locations (fig. 5) and large-horn major-morph *C. atlas* had longer horns than small-horn major *C. caucasus* in many sympatric locations. However, there was no overlap of genitalia size between the two species in any of the sympatric locations, the smallest genitalia of *C. caucasus* being always larger than the largest

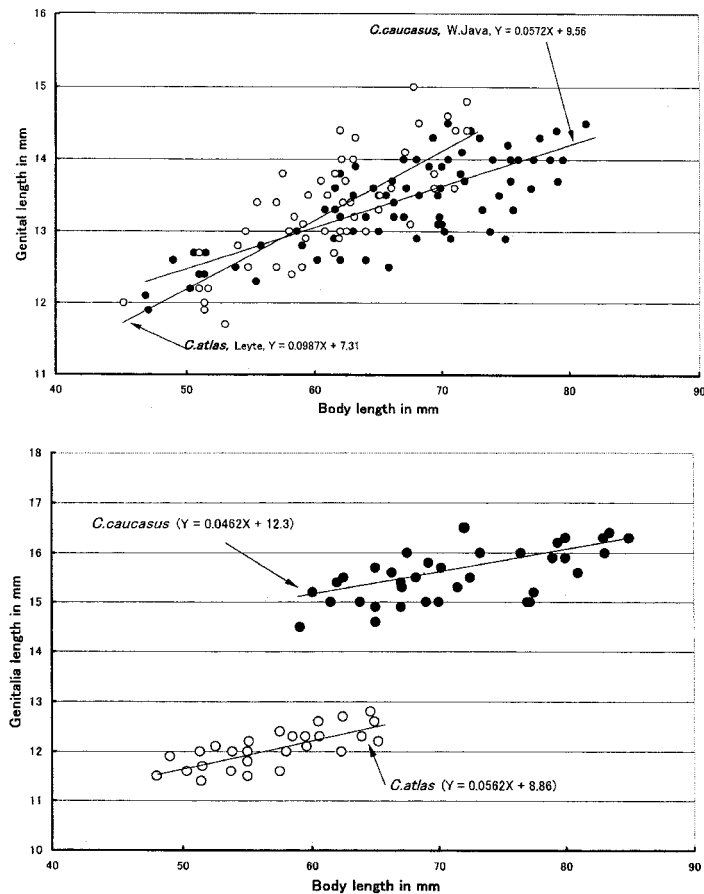


Figure 6: *Top*, relationship between body length and genitalia length of *Chalcosoma caucasus* in West Java and *Chalcosoma atlas* in Leyte, where each is allopatric from the other. Note that the dimensions of the two species overlap with each other. *Bottom*, relationship between body length and genitalia length of *C. caucasus* and *C. atlas* in a sympatric location (South Sumatra). Note that the dimensions of the two species are far apart without any overlap.

genitalia of *C. atlas* (fig. 7). Thus, the character displacement in sympatry of the male genitalia was most extreme.

Intraspecific Variation in Allopatry and Sympatry

ANOVAs comparing allopatric and sympatric populations for intraspecific variability revealed no significant differences in either species (table 3). There was no sign of intraspecific variation being compacted in sympatry. I thus conclude that the character displacement in sympatry took place without changing intraspecific variability in morphology.

Separation of Uncontrollable Ecological Effects from Allopatry/Sympatry Effects

Measurement of difference between two species in allopatry requires at least two separate locations and that in

sympatry requires another location. If all these locations are endowed with the same ecological conditions, a simple comparison between allopatry and sympatry gives a straight measure for the occurrence of character displacement. On the one hand, the ecological conditions vary from one location to another, and a simple comparison in character state between sympatric and allopatric locations includes not only true effect of allopatry/sympatry but also other ecological factors such as random geographic and climatic effects, predation, or parasitism. On the other hand, the variation only within allopatry or only within sympatry represents possible ecological effects other than the allopatry/sympatry effect. If the sampling locations within allopatry or sympatry are many and comprehensively cover the ecological conditions of both species habitats, the mean of several locations should be

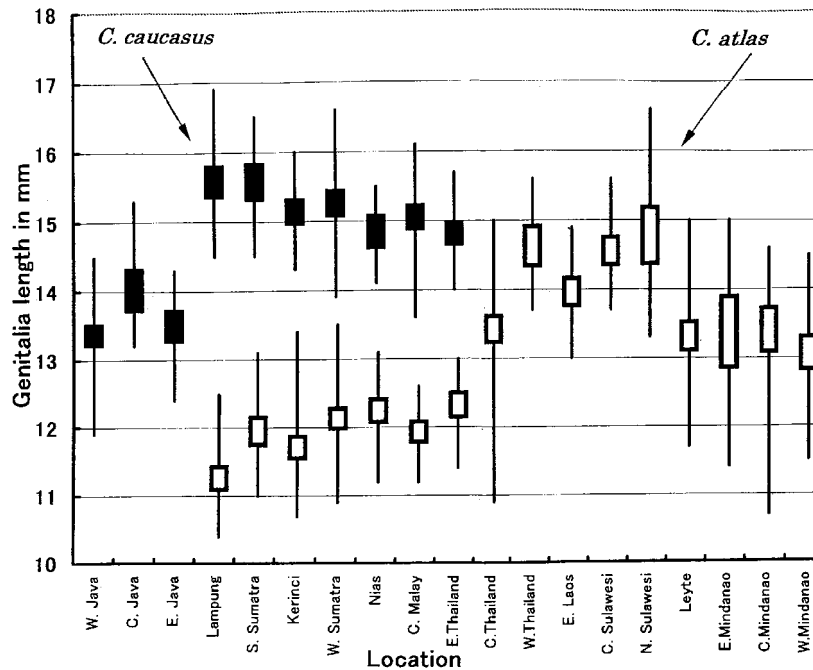


Figure 7: Genitalia length of *Chalcosoma caucasus* and *Chalcosoma atlas* in allopatric and sympatric locations. The 5% reliable range of mean of each population is shown by a rectangular box, and the maximum and minimum values are shown by a vertical line.

representative for allopatry or sympatry, respectively. Insofar as I know, the sample locations of this study are distributed throughout the entire geographical range and include a random sample of ecological habitat diversity of both species. In addition, larvae of both species grow in leaf and tree humus and the adult beetles depend on tree sap and other plant exudations for their energy resources (Unno 1993). These nutritional and energy sources are nonspecific to certain flora and broadly available throughout the tropics (e.g., Mizunuma 1999). Thus, the samples are representative of the species.

In the ANOVAs in tables 3 and 4, I used mean squares corresponding to variation within allopatry or sympatry as the basis of error for measuring the allopatry/sympatry effect, and the number of both allopatric and sympatric locations was large enough to permit an effective ANOVA. Thus, the ANOVAs here were not only valid statistically but also effectively separated the allopatry/sympatry effect from other ecological effects. The results effectively eliminate the possibility of body-size shifts in these species occurring by uncontrollable ecological effects and support the conclusion that the phenotypic body-size displacement of *C. caucasus* and *C. atlas* at sympatry took place in response to the presence of the other species.

Quantification of Phenotypic Character Displacement

Following the established understanding (Grant 1972; Futuyma 1986), the ratio (difference between two species in sympatry)/(difference between the two species in allopatry) should give a quantitative measure of the degree of character displacement attributable to competition or interaction between the two species in sympatry. The actual figures, given by $(C.c. - C.a. \text{ in sympatry}) / (C.c. - C.a. \text{ in allopatry})$ or S/A in table 2, were distinctly greater in genitalia length than in body length or head horn length.

Similarly, $[(C.c. - C.a. \text{ in sympatry}) - (C.c. - C.a. \text{ in allopatry})] / \text{mean character value}$, or $(S - A)/M$ in table 2, provides the relative magnitude of sympatric effect in each character, and this may be the best biological measure for sympatric character displacement. Character displacement was 24% of mean genitalia length, 16% in body length, and 18% in head horn length (table 2). This indicates that the degree of displacement in sympatry was greatest for genitalia length.

Furthermore, $[(C.c. - C.a. \text{ in sympatry}) - (C.c. - C.a. \text{ in allopatry})] / \text{intrapopulation SD}$ in each character (mean of all locations) measures the magnitude of sympatric effect relative to the variability of each character. This was 5.32,

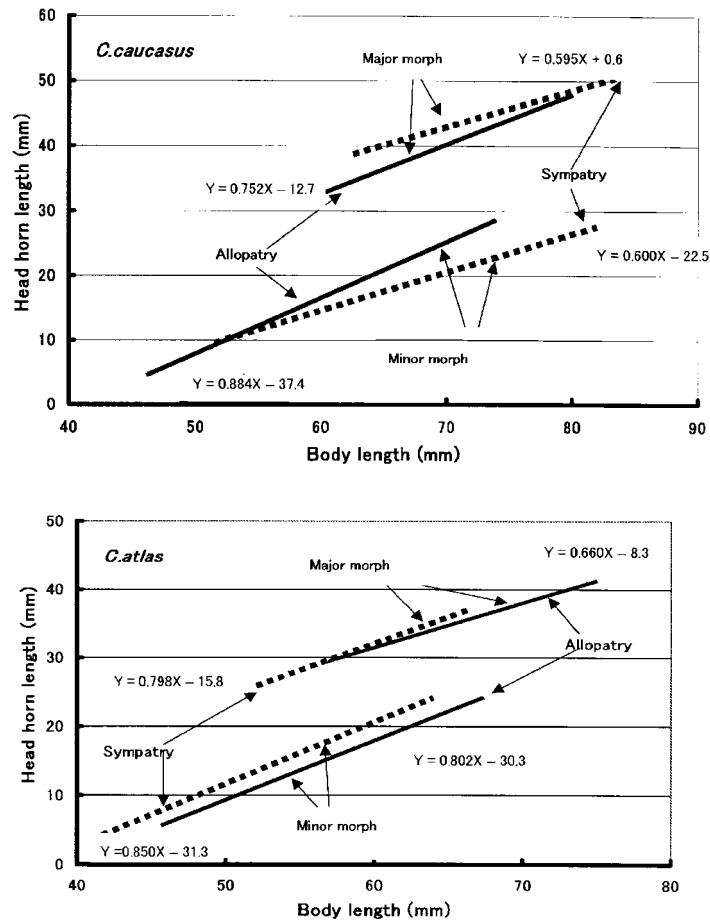


Figure 8: Comparison in regression of head horn length on body length between allopatry and sympatry in major and minor morphs in *Chalcosoma caucasus* (top) and *Chalcosoma atlas* (bottom).

1.53, and 0.39 for genitalia length, body length, and head horn length, respectively. Here, again, the magnitude of sympatric effect was distinctly great on genitalia size.

Allopatry/Sympatry Effect on Regression on Body Size

Regression of head horn length on body length in major and minor morphs in allopatry and sympatry (all the locations within the same patry were lumped together) in each species indicated that there was no great difference in intercept or slope between allopatry and sympatry in both species (fig. 8). While a large proportion (43%–72%) of the variance of head horn length was accounted for by the total regression, only <3.6% was attributable to the patric effect (table 5). This suggests that largely the same relationship of body length with head horn length persisted between allopatry and sympatry.

There was no appreciable difference in the relationship

of body length to genitalia length between major and minor morphs in either species, and, hence, the individuals of the two morphs were lumped together for analyzing the relationship of body length with genitalia length. There was a statistically highly significant difference (mostly in intercept) in the regression of genitalia length on body length between allopatry and sympatry in both species (fig. 9). While a significant proportion (45%–55%) of the variance of genitalia length was accounted for by the regression on body length, an equally significant portion (38.9% in *C. caucasus* and 15.4% in *C. atlas*) of genitalia length variance was attributable to the patric effect (table 5). This suggests that the relationship of body size with genitalia size was fundamentally altered by the allopatry/sympatry effect.

Except for the regression of head horn length on body length in the major morph, the proportion of unaccountable variance was low (e.g., 12.3% in the genitalia regres-

Table 5: Partition of head horn length and genitalia length variances in *Chalcosoma* species attributable to allopatry/sympatry effects in their regression on body length

| Species/character/ morph | Total regression | Allopatry/sympatry effect on | | Location (intrapatry) effect on | | Unaccountable variation |
|------------------------------|---------------------|-------------------------------------|--------------------------------------|-------------------------------------|--------------------------------------|----------------------------|
| | | Height of regression (intercept) | Regression coefficient (slope) | Height of regression (intercept) | Regression coefficient (slope) | |
| <i>C. caucasus</i> head | | | | | | |
| horn length: | | | | | | |
| Major | 43.3** | .8* | .3 | 3.6** | 5.2** | 46.7 |
| Minor | 54.6** | 2.3** | 1.3** | 6.8** | 5.3** | 29.7 |
| <i>C. atlas</i> head horn | | | | | | |
| length: | | | | | | |
| Major | 43.8** | .4 | .0 | 10.0** | .0 | 45.9 |
| Minor | 71.8** | 2.0** | .0 | 1.3** | 6.0** | 18.8 |
| <i>C. caucasus</i> genitalia | | | | | | |
| length, all | | | | | | |
| morphs | 44.5** | 38.9** | .0 | 3.9** | .5* | 12.3 |
| <i>C. atlas</i> genitalia | | | | | | |
| length, all | | | | | | |
| morphs | 54.5** | 14.3** | 1.1** | 16.8** | 1.2** | 12.3 |

* Statistically significant difference at .05.

** Statistically significant difference at .01.

sion; table 5), indicating that body size and patry are sufficient to account for most of the variation. A visual comparison of *C. caucasus* and *C. atlas* in allopatry and sympatry clearly demonstrates the result of the analyses mentioned above (fig. 4).

Discussion

Examining scattered cases of alleged character displacement, Futuyma (1986) sorted out the following conditions for the unambiguous establishment of character displacement caused by species interaction in sympatry: character state in sympatry is different from that in allopatry; character difference between two species in sympatry is larger than that in allopatry; and separation of allopatry/sympatry effect from random ecological effects. There have been few cases where all of these conditions were supported by rigorous statistical tests. This study offers a case of character displacement confirmed with respect to all the conditions above and beyond any statistical doubt. Thus, the case of *Chalcosoma caucasus* and *Chalcosoma atlas* may be a most complete, most illustrative example of sympatric character displacement.

In rhinoceros beetles (Tribe Dynastini, Subfamily Dynastinae, Family Scarabaeidae) including the *Chalcosoma* species, major morph males, or large-body males with large horns, are often seen in direct physical combat with other major males of the same species attempting to secure a mating female. Minor morph males, or small-body males with rudimentary horns and comparatively large wings,

secure mating opportunities by emerging earlier in the season, appearing earlier in the day, flying longer distances, and avoiding physical confrontation with major morph males (Beebe 1944; Eberhard 1980, 1982; Cook 1987; Siva-Jothy 1987; Kawano 1991, 1992; Unno 1993). The rich intraspecific variability is caused primarily by the nutritional conditions during the larval period and is considered to be an effective mechanism for tolerance to fluctuating environmental conditions (Eberhard 1980; Emlen 1994; Iguchi 1998). The great differentiation of both body and head horn sizes between the major morph males of the *Chalcosoma* species in sympatry may have taken place to avoid interspecific physical combat. The equally great differentiation of body size but less great differentiation of horn length between the minor morph males of these species may have occurred to avoid habitat duplication rather than to avoid physical combat. Thus, the displacement as a whole may function to reduce interspecific competition for resources and mates.

Male genitalia of rhinoceros beetles (penis; the part used for the quantitative measurement in this study) are composed of three parts—basal, middle, and apical. During copulation, the male mounts the female from behind, locking her underneath, and thrusts his penis toward the abdominal end of the female. The apical part of the penis clutches the female vagina and the middle part bridges between the male and female bodies, through which the ejaculation duct passes and the sperm is injected into the female body. Thus, the physical length of genitalia may be important for mating success. The fact that character dis-

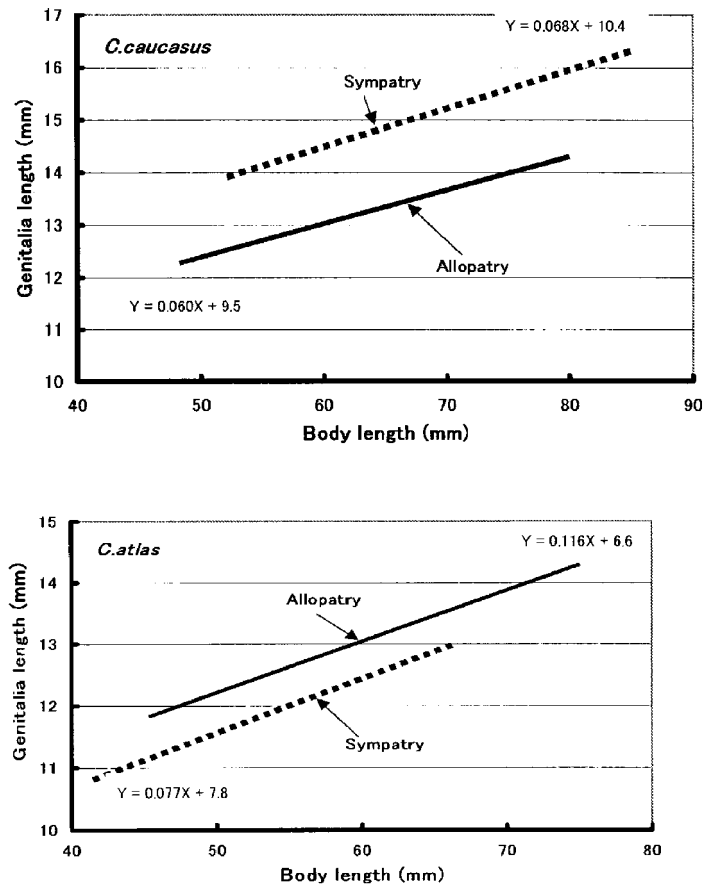


Figure 9: Comparison in regression of genitalia length on body length between allopatry and sympatry in *Chalcosoma caucasus* (top) and *Chalcosoma atlas* (bottom).

placement in sympatry was greatest and most complete in genitalia length suggests that reproductive isolation is an important factor in interspecific interaction in sympatry. Allometry of sexually related characters in insects can be altered by selection (Wilkinson 1993) and male genital morphology of beetles can be highly sensitive to interspecific interaction (Eberhard 1990). These results are empirical evidence of these processes acting in nature.

Body size is determined by the interaction of the genetic capacity for growth with the nutritional condition of the environment, including the length of larval period. The observations (though no statistically analyzable hard data are available) that *C. caucasus* tends to occur at higher altitudes and *C. atlas* at lower altitudes in sympatric locations than in allopatric locations suggest the possibility that the observed sympatric displacement in body size and external morphology may be caused by a change in female oviposition patterns, which lead to differential body-size development at different temperatures. The unaltered de-

velopmental relationship of body length with head horn length between allopatry and sympatry (fig. 6; table 5) favors this possibility. The morphological displacement in this case may have been caused by habitat differentiation and may not be genetic.

The degree of genitalia length displacement far exceeded what was expected from the general body-size displacement and the developmental relationship of body length to genitalia length was radically different between allopatry and sympatry (fig. 8; table 5). This suggests that the sympatric displacement of genitalia size took place not as a result of body-size adaptation to habitat differentiation but was caused by factors other than habitat differentiation.

Regarding the question of how these species have come to this status, I can describe three possible scenarios. The most orthodox interpretation is that these species evolved allopatrically and, by range expansion, have come to coexist in sympatric locations through morphological displacement and behavioral adjustment. Under this scenario,

character displacement is a result of competition between existing species.

The second scenario starts from a sympatric speciation event in the same location. With the geographic habitat expansion of the resulting species, some locations stayed sympatric while others became allopatric. Under this scenario, divergent or disruptive selection induces speciation, and hence, the two species are the result, not the cause, of character displacement. There is experimental evidence that competition promotes divergence in adaptive radiation (Schluter 1994, 1996; Orr and Smith 1998).

There have been cases where morphologically different species occurring in the same geographical area were found to be phylogenetically closer to one another than to the same or morphologically similar species occurring in different locations (Lake Victoria cichlid fishes [Meyer et al. 1990]; *Heliconius* butterflies [Brower 1994]; giant senecios plants [Knox and Palmer 1995]; *Ohomopterus* ground beetles [Su et al. 1996]; *Anolis* lizards [Losos et al. 1998]). Particularly surprising among these is the *Ohomopterus* ground beetle, where sympatrically occurring different species, distinguished by different genital morphology, were found to be phylogenetically closer with each other than to the same species, described with identical or very similar genitalia morphology but occurring in other locations (Su et al. 1996). This lays the groundwork for the third scenario, that the two *Chalcosoma* species in each sympatric location might be phylogenetically closer to each other than to the same species in other locations. In other words, the population of the two species in each sympatric location constitute a phylogenetically independent unit, inevitably suggesting that *C. caucasus* and *C. atlas* evolved many times independently in each sympatric location. The same features of the two species maintained throughout all seven sympatric locations makes it unlikely that the differences are the result of seven sympatric speciation events. Nevertheless, the extensive geographic sympatry of these species further provides a unique opportunity for studying the biological significance of interspecific interaction in speciation.

The remarkable consistency in qualitative characters of each species makes *C. caucasus* and *C. atlas* good morphological species defined by traditional taxonomy. The clear differentiation between the two species in habitat, external morphology, and genitalia size makes them good biological species as defined by Mayr (1957, 1988). *Chalcosoma caucasus* and *C. atlas* are behaviorally definable biological entities. Whether the origin of these two species followed the first or the second scenario, each species behaves as an integrated unit.

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