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Sexual and Male Horn Dimorphism in *Copris ochus* (Coleoptera: Scarabaeidae)

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Copris ochus (Coleoptera: Scarabaeidae), an endangered species, is the largest dung beetle in Japan. In *C. ochus*, males have a long head horn, while females lack this long horn (sexual dimorphism). Very large males of *C. ochus* have disproportionately longer head horns than small males, suggesting male horn dimorphism, although the dimorphism has not been investigated quantitatively. To clarify sexual and male horn dimorphism in *C. ochus* quantitatively, we examined the scaling relationship between body size (prothorax width) and head horn length in 94 females and 76 males. These beetles were captured during July 1978 from a natural population on Mt. Aso in southwestern Japan using a light trap. Although the horn length of the females and males scaled with prothorax width, the scaling relationship differed between the sexes, *i.e.*, the relationship was linear in females and nonlinear in males. Statistical tests for dimorphism in male horn length showed a significant discontinuous relationship, thus indicating distinct sexual and male dimorphism in head horns. Long- and short-horned *C. ochus* males may have different reproductive behaviors, as described in other horned dung beetles.

Key words: discontinuous, linear, major/minor morph, male horn dimorphism, scaling relationships

INTRODUCTION

The exaggerated horns and mandibles of beetles have fascinated biologists for centuries, including Darwin and Wallace (*e.g.*, Otte and Stayman, 1979). Species with extraordinary horns or mandibles are also characterized by extreme variation in morphology, such that not all individuals express the trait to the same extent (Eberhard and Gutiérrez, 1991; Emlen and Nijhout, 2000). The exaggerated horns or mandibles can be expressed in one sex only (sexual dimorphism; Emlen and Nijhout, 2000), such as the huge mandibles of soldier ant castes (all females) or the enlarged horns or mandibles of beetles (generally all males). Horn or mandible size often scales with body size, and larger individuals possess horns or mandibles that are much longer in length compared to those of smaller individuals (Emlen and Nijhout, 2000). Such intrasexual morphological dimorphic forms are known as major/minor morphs, and are seen in horned beetles (Eberhard, 1980) and female ants (Hölldobler and Wilson, 1990). Exaggerated head or thorax horns are frequently found in the beetle family Scarabaeidae, and dimorphism in male horns has evolved independently multiple times within this family (Emlen and Nijhout, 2000).

Copris ochus (Motschulsky) (Coleoptera: Scarabaeidae) is the largest dung beetle in Japan (Hori, 2005; body length, 18–34 mm; Fig. 1). Males of *C. ochus* have a long head

horn, while females lack such a long horn (sexual horn dimorphism; Fig. 1). Very large *C. ochus* males have disproportionately longer head horns than small males (Ochi, 1985; Coprophagous Group, 2005; Fig. 1B–G), suggesting male head horn dimorphism, although the dimorphism has not been investigated quantitatively. *Copris ochus*, which feeds on the dung of large mammals, is distributed in Japan, the Korean Peninsula, Mongolia and China (Ochi, 1985). *Copris ochus* was once common in Japanese stock farms (Ochi, 1985). In recent years, however, Japanese populations of *C. ochus* have been declining (Coprophagous Group, 2005), which may be attributable to a decrease in stock farms or cattle and the negative effects of the antiparasitic drugs given to cattle on the survival of *Copris* beetles (Wardhaugh and Rodriguez-Menendez, 1988; Hori, 2005). Therefore, *C. ochus* has been identified as a near-threatened (NT) species in the Japanese Red Data Book (Ministry of the Environment of Japan, 2006). To assist in its conservation, the biology and ecology of *C. ochus* should be generally known (*e.g.*, Bang *et al.*, 2004).

Although one must use several specimens to examine dimorphism in the male horns of *C. ochus*, it is now difficult to collect many individuals of this endangered species in the field. Although collected museum specimens may be available, as Emlen and Nijhout (2000) suggested, museum specimens are always collected at a variety of times and sites, incorporating collector bias for certain sizes, as well as geographic variation. Therefore, when examining horn dimorphism, it is important to collect samples randomly at a particular season from a local population (Emlen and Nijhout, 2000).

Here, we tested the sexual and male horn dimorphism

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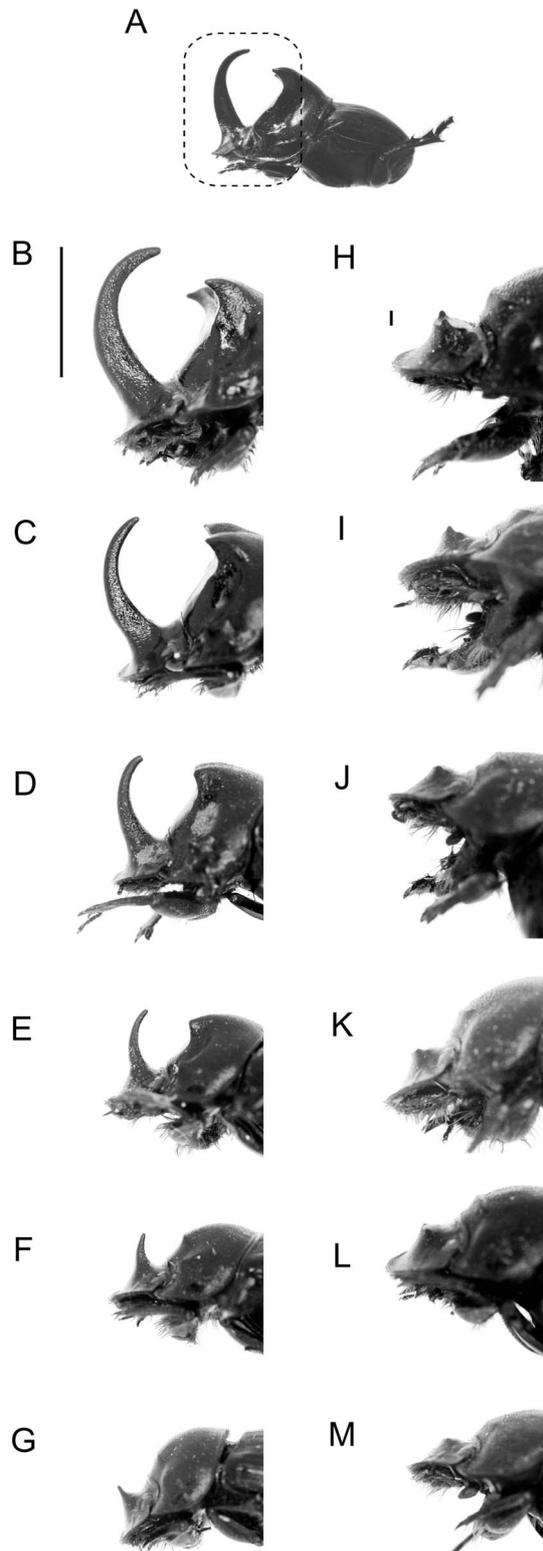


Fig. 1. Lateral views of *Copris ochus*. (A) Male body. (B–G) Male heads and prothoraxes. (H–M) Female heads and prothoraxes. The respective prothorax and head horn lengths (mm) are (A) 15.2 and 10.3, (B) 15.2 and 9.9, (C) 14.3 and 8.5, (D) 13.3 and 6.8, (E) 12.8 and 4.0, (F) 11.9 and 3.2, (G) 10.9 and 1.9, (H) 14.7 and 1.4, (I) 13.7 and 1.3, (J) 12.6 and 0.9, (K) 12.5 and 0.9, (L) 11.75 and 0.7, and (M) 10.2 and 0.6. The bars (B, H) show the head length from the tip of the horn to the dorsal surface of the head immediately posterior to the horn.

of *C. ochus* by analyzing the scaling relationship between body size and horn length. The specimens were collected by the third author from a Japanese population during a single season in 1978, when *C. ochus* was common in Japan. We discuss an aspect of the behavioral ecology of *C. ochus*.

MATERIALS AND METHODS

Methods

To examine the relationship between body size and horn length of *C. ochus*, we examined 94 females and 76 males that the third author collected using a light trap (Kuranaga-Morimoto type; Baba and Hirashima, 1991) at a location (32°52' N, 131°4' E; 1,110 m elevation) on Mt. Aso, Kumamoto Prefecture, southwestern Japan, over two weeks from late June to early July 1978. Therefore, these represent a sample from one population during one season, although a light trap may not attract all individuals equally. When this sampling was conducted, *C. ochus* was common in Japanese stock farms (Ochi, 1985).

Copris ochus exhibits sexual dimorphism in head horns (Ochi, 1985; Coprophagous Group, 2005): *C. ochus* males have one horn on the head (Fig. 1A–G), while females have a different type, which is called a transverse carina rather than a horn (Fig. 1H–M). To examine the scaling relationship between body size and horn length, we measured the prothorax length and head horn length of *C. ochus* to the nearest 0.1 mm using slide calipers. We used an ocular micrometer in a dissecting microscope to measure the horn length of females to the nearest 0.1 mm, because female head horns are small, ranging in size from 0.5 to 1.7 mm (Fig. 1H–M). All of the measurements were straight-line distances between two clearly defined reference points. Head horn length was measured from the tip of the horn to the dorsal surface of the head immediately posterior to the horn (Fig. 1B, H), in the same manner as Eberhard and Gutiérrez (1991) measured male head horn length in the congeneric species *Copris lugubris* Boheman.

Analysis

We used the Shapiro-Wilk W test in testing normality of natural variation in prothorax width and horn length (Crawley, 2007: 281–282). To clarify the dimorphism of horn length in *C. ochus*, we used the statistical tests proposed by Eberhard and Gutiérrez (1991), which involve a combination of techniques. First, the following regression model was fitted:

$$Y^* = \alpha_0 + \alpha_1 X^* + \alpha_2 X^{*2} + \varepsilon \quad (\text{Model 1})$$

in which Y^* is the natural log of horn length; X^* is the natural log of a measure of body size, such as prothorax width; α_i are the regression coefficients; and ε is a random component with an assumed normal distribution, mean of zero, and common variance.

If the coefficient α_2 was not significantly different from zero, then further analysis was not justified, as the relationship did not deviate significantly from linearity. If α_2 was significant, a hypothesis regarding possible switching mechanisms was then tested. This hypothesis had two components: the linear slope of horn (Y) versus body size (X) changes at some switch point in the range of measured body sizes, and the change in Y at the switch point is discontinuous rather than continuous. To test the discontinuity hypothesis, the following piecewise regression model was used:

$$Y = \beta_0 + \beta_1 X + \beta_2 (X - X^0)D + \beta_3 D + \varepsilon \quad (\text{Model 2})$$

in which Y and X are in actual measurement units; X^0 is the proposed switch point; $D=0$ if $X < X^0$, otherwise $D=1$; β_i are the regression coefficients; and ε is a random component with an assumed normal distribution, mean of zero, and common variance.

To determine which switch point gave the best fit, 30 different values were substituted in Model 2 for the switch point (X^0 : from 11.0 to 16.8 mm at 0.2-mm intervals), and the adjusted R^2 was cal-

culated for each. The adjusted R^2 values were then plotted against the possible switch points, and fitted to a fifth-degree polynomial (quasicubic spline). The X^0 value (switch point) giving the maximum value of the adjusted R^2 was determined visually. If the coefficient β_3 in Model 2 differs significantly from zero, the switch point exists. If the coefficient β_2 in Model 2 differs significantly from zero, the slope changes at the switch point.

All of the statistical tests were conducted at the 0.05 level of significance. We conducted all of the statistical analyses using R ver. 2.4.1 (R Development Core Team, 2006). We fitted the piecewise regression model following Crawley (2007: 603).

RESULTS

Natural variation in prothorax width and horn length did not differ significantly from a normal distribution in females (Shapiro-Wilk W test; prothorax width, $W=0.98$, $P>0.05$; horn length, $W=0.98$, $P>0.05$; Fig. 2A). The relationship between prothorax width and horn length appeared linear in females (Fig. 2A). In Model 1, coefficient α_2 was not significantly dif-

ferent from zero ($\alpha_2=-0.24\pm 1.13SE$, $t=-0.21$, $P=0.84$), indicating that the relationship was not significantly different from linearity (Fig. 2A). Natural variation in prothorax width did not differ significantly from a normal distribution in males ($W=0.98$, $P>0.05$; Fig. 2B). However, natural variation in horn length was not normally distributed in males ($W=0.94$, $P=0.0017$; Fig. 2B). The relationship between prothorax width and horn length was not linear in males (Fig. 2B). In Model 1, coefficient α_2 was significantly different from zero ($\alpha_2=-8.01\pm 2.39SE$, $t=-3.35$, $P<0.01$), indicating that the relationship differed significantly from linearity. The switch point (X^0) value that gave the maximum adjusted R^2 value was 13.0. At this best switch value, coefficient β_3 in Model 2 differed significantly from zero ($\beta_3=1.48\pm 0.29SE$, $t=5.12$, $P<0.01$), indicating that the relationship was discontinuous. Furthermore, coefficient β_2 in Model 2 was not significantly different from zero ($\beta_2=0.13\pm 0.28SE$, $t=0.48$, $P=0.64$), indicating that the slope did not change significantly over the switch point (Fig. 2B).

DISCUSSION

We found a distinct difference in the scaling relationship between body size and head horn length between the two sexes: the horns of *C. ochus* females scaled linearly with prothorax width, while those of males did not (Fig. 2). Therefore, we could detect sexual dimorphism, but not female dimorphism in the head horns of *C. ochus*, as suggested in previous studies (Ochi, 1985; Coprophagous Group, 2005).

The male horn length of a dung beetle species depends on nutrient conditions or the amount of food obtained during the larval period, rather than on the length of the father's horn (Emlen, 1994, 1997a). In dung beetles, the pattern of the scaling relationship between body size and horn length can differ among species within the same genus (Emlen and Nijhout, 2000; Emlen *et al.*, 2005), and Emlen *et al.* (2005) indicated that male horn dimorphism had been lost independently multiple times from the horned ancestor species of a dung beetle genus.

Eberhard and Gutiérrez (1991) examined the scaling relationship between prothorax width and male head horn length for *C. lugubris* (a congener of *C. ochus*) using the same statistical tests as we used. They found a nonlinear relationship between prothorax width and horn length in *C. lugubris* males ($\alpha_2=-25.45$, $t=-10.13$, $P<0.001$ in Model 1), but could not detect discontinuity of the scaling relationship (β_3 was not significantly different from zero, $P=0.853$ in Model 2; Eberhard and Gutiérrez, 1991). Therefore, no significant evidence of horn length dimorphism was detected in *C. lugubris* males. In this study, we not only found a nonlinear relationship between prothorax width and horn length in *C. ochus* males, but also discontinuity in this scaling relationship (Fig. 2B). This is significant evidence of horn length dimorphism in *C. ochus* males. Males of horned beetles use their horns when fighting other males for mates; females choose mates (*e.g.*, Eberhard, 1980). Therefore, the differential pattern of the scaling relationship between prothorax width and horn length may be related to differences in reproductive behavior between *C. lugubris* and *C. ochus*.

Studies of horned beetle species have shown that long- and very short-horned males often have different reproductive behaviors (Emlen, 1997b). For example, a horned dung

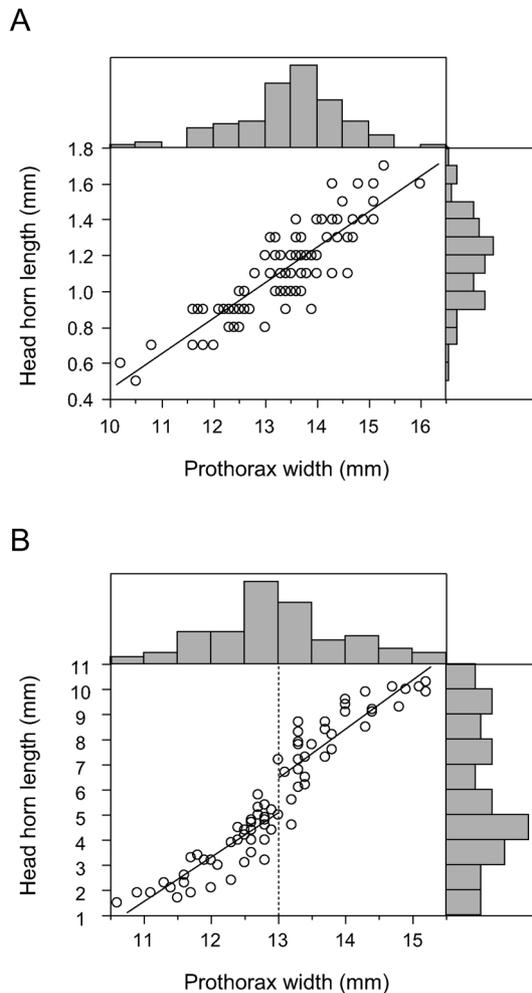


Fig. 2. Scaling relationship between prothorax width and horn length for (A) 94 females and (B) 76 males of *Copris ochus*. Histograms of prothorax width and horn length are also shown. The dotted line on the horn axis indicates the switch point (see text). The solid lines in (A) and (B) are the fitted linear regression [A; $Y=-1.52+0.20X$] and the piecewise regression model [B; $Y=-17.80+1.76X+0.13(X-13.0)D+1.48D$], respectively.

beetle species with two male morphs has different mating behaviors during encounters with females: large, long-horned males, which guard entrances to tunnels containing females, fight with all other males that attempt to enter these tunnels, while small, hornless (or short-horned) males encounter females by sneaking into tunnels guarded by other males (Emlen, 1997b). Females of the genus *Copris* excavate an underground nest and take care their offspring in dung balls that they make (*i.e.*, subsociality; Klemperer, 1982a, b; Tyndale-Biscoe, 1984; Bang *et al.*, 2004). *Copris* males assist their mates in preparing dung pellets and in excavating the nest, and remain in the nest until after the female completes oviposition (Klemperer, 1982b). Therefore, *Copris* males may defend females against other males, although combat among males has not been fully observed. *Copris ochus* had distinct dimorphism of male horn length (Fig. 2B). Although the behavior of *C. ochus* males has not been examined, long- and short-horned males of *C. ochus* may have different reproductive behaviors, as described for other horned dung beetles. Observations of male behavior in *C. ochus*, which is now endangered in Japan, are needed to test this hypothesis.

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