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Horn Dimorphism of *Allomyrina dichotoma septentrionalis* (Coleoptera: Scarabaeidae) Affected by Larval Nutrition

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ABSTRACT I reared larvae of a dimorphic horned beetle, *Allomyrina dichotoma septentrionalis* (Kono), under 2 different conditions and measured the horn length and body length of male adults obtained from those larvae. Adults from well-nourished larvae showed a bimodal frequency distribution of horn length, but adults from ill-nourished larvae did not. The allometric relationship between horn length and body length differed significantly between ill-nourished and well-nourished larvae. The results suggest that adults from ill-nourished larvae develop their bodies more fully than their horns, and that adults from well-nourished larvae develop their horns more fully than their bodies. I conclude that the horn dimorphism of this beetle arises from differences in the level of larval nutrition.

KEY WORDS *Allomyrina dichotoma septentrionalis*, dimorphism, allometry, nutrition

PAST STUDIES OF horned beetles have shown that large males usually have larger horns than small males, and that some species are dimorphic for horn size and show bimodality in the frequency distribution of horn size (Eberhard 1980, 1982, 1987; Cook 1987; Siva-Jothy 1987; Eberhard and Gutierrez 1991; Kawano 1995a, b). Because horned beetles are holometabolous, adult size depends on larval size and does not vary in their lifetimes. Therefore, male dimorphism of horned beetles has been supposed to arise from differences in quality and quantity of larval food (Eberhard 1980, 1982; Cook 1987). Emlen (1994, 1996, 1997) and Moczek and Emlen (1998) have already demonstrated that larval nutrition affects adult males in the genus *Onthophagus*. However, there have been no experimental studies in dynastine horned beetles.

I reared larvae of a Japanese dimorphic horned beetle, *Allomyrina dichotoma septentrionalis* (Kono), under 2 different conditions. The behavior and ecology of this beetle already have been studied in detail (Obata and Hidaka 1983; Siva-Jothy 1987; Tsurumaki 1987; Uémura 1987; Iguchi 1996, 1997; Yoshida 1996). In this article, I discuss the influence of larval nutrition on the adult horn dimorphism of this beetle.

Materials and Methods

The life cycle of *A. d. septentrionalis* lasts ≈ 1 yr. Adults usually emerge in July and August in Okaya, where this study was conducted. They lay eggs on humus in the soil. Larvae feed on humus and develop to the 3rd instar in ≈ 40 d (Tsurumaki 1987, Uémura

1987). The final instars overwinter and pupate in the soil in June and July the next year. The pupae become adults in ≈ 20 d (Tsurumaki 1987, Uémura 1987).

Male adults for this study were obtained from 2 experiments. In the 1st experiment (A), 81 final instars (≈ 4 –5 cm long) were randomly collected in the soil near a forest of assorted trees in the western part of Tatsuno-machi, Kamiina-gun, Nagano Prefecture on 30 September 1990. The soil was dark, soft, moist humus that contained many chips of decayed wood. The larvae were put in 3 wooden boxes (27 larvae in each box) of the same size (30 cm wide, 64 cm long, 31 cm high) with the soil (≈ 59 liters) in which they had lived. Each box was covered with a wooden board and placed outdoors. No more humus or soil was added throughout the experiment, but water was sprinkled to keep the soil moist.

In the 2nd experiment (B), 81 nearly fully grown final instars (≈ 8 –10 cm long) were randomly collected at the same site as in experiment A on 13 June 1992. Experiment B was carried out in the same way as in experiment A.

Male *A. d. septentrionalis* have a long head horn and a shorter prothoracic horn. I measured the length of the head horn and the length of the body excluding the horns to 0.5 mm with a slide caliper (Fig. 1).

I expected that the humus in each box would be less sufficient for the larvae in experiment A than for those in experiment B, because experiment A would last far longer than experiment B. Therefore, I expected that smaller males would emerge in experiment A than in experiment B.

I have deposited voucher specimens of this horned beetle in the Kamiina-kyodokan (Kamiina Local Mu-

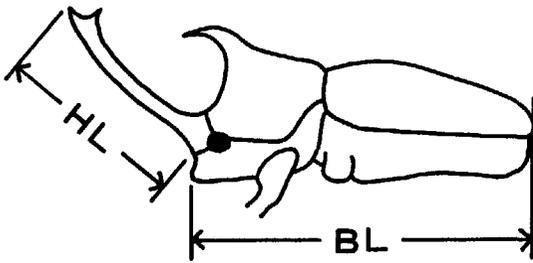


Fig. 1. Lateral view of male *A. d. septentrionalis* showing dimensions measured. HL, horn length; BL, body length.

seum, 3520, Sakuramachi, Ina City, Nagano Prefecture, 396-0021, Japan) near the study site.

Results

In experiment A, 18 males and 22 females emerged between 10 and 24 August 1991. In experiment B, 31 males and 39 females emerged between 31 July and 10 August 1992. There were no significant differences in the sex ratio between the 2 experiments ($\chi^2 = 0.0161$, $df = 1$, $0.8 < P < 0.9$).

The males in experiment A were significantly smaller than those in experiment B in both body length and horn length (Mann-Whitney *U*-test, $P < 0.001$ for both) (Figs. 2 and 3).

Using the original values of body length and horn length, I obtained the regression lines $y = 0.46x - 8.30$ for experiment A and $y = 1.08x - 27.71$ for experiment B, where x and y are body length and horn length, respectively. The regression slope for experiment B was significantly steeper than that for experiment A ($t = 2.790$, $df = 45$, $P < 0.005$). However, it was not clear whether the plotted data were discontinuous between the 2 experiments. Therefore, I used loga-

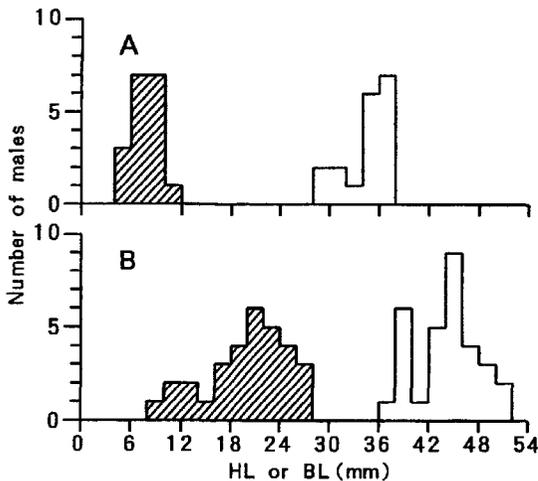


Fig. 2. Frequency distributions of horn and body lengths. (A) Experiment A, 18 males. (B) Experiment B, 31 males. Shaded areas, horn length; unshaded areas, body length.

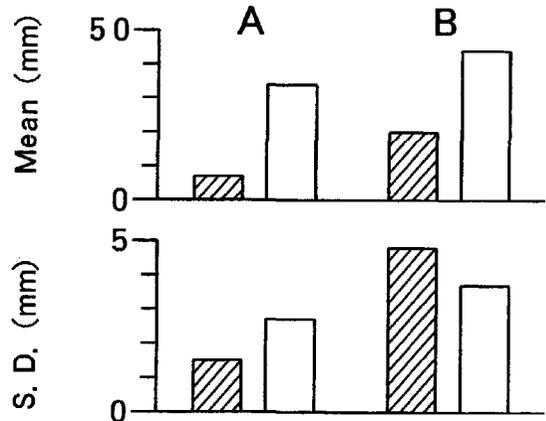


Fig. 3. Arithmetic mean and standard deviation of horn and body lengths. (A) Experiment A, 18 males. (B) Experiment B, 31 males. Shaded areas, horn length; unshaded areas, body length.

arithmic transformation to examine whether the data from both experiments were scattered along the same allometric curve.

Fig. 4 shows horn length plotted against body length on logarithmic scales. The regression of log horn length on log body length in each experiment was highly significant (experiment A, $t = 6.441$, $df = 16$, $P < 0.001$; experiment B, $t = 8.542$, $df = 29$, $P < 0.001$). The 2 regression lines did not differ significantly in slope ($t = 1.061$, $df = 45$, $0.2 < P < 0.3$), but they were significantly expressed as 2 separate lines by analysis of covariance ($P < 0.001$). The regression line for experiment B lies above that for experiment A.

Discussion

A serious problem may occur in experiments of this type—whether the length of the larval stage affects

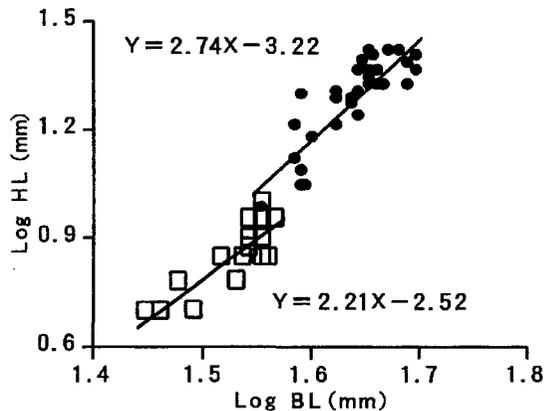


Fig. 4. Linear regressions of logarithmic horn length (log HL) on logarithmic body length (log BL). □, experiment A, 18 males; ●, experiment B, 31 males.

adult size. In experiment B, large males emerged later than small ones (I report this result in detail elsewhere). On the other hand, the males in experiment A emerged later than field males in the same year. However, all the males in experiment A were small. These results suggested that the 2 male morphs were not the result of differences in the length of the larval stage.

Tsurumaki (1987) mentions that >5 final instars cannot be fully reared in a container (30 by 30 by 30 cm). This means that 1 final instar needs \approx 5 liters of humus. Yoshida (1996) also mentions that 1 larva needs \approx 3 liters of humus. In both my experiments, however, the amount of humus per larva was \approx 0.7 liters. Experiment B lasted \approx 50 d, but experiment A lasted \approx 320 d. Therefore, it is reasonable to suppose that the humus in each box was less sufficient for the larvae in experiment A than for those in experiment B.

The untransformed regressions for the 2 experiments showed that horn length increased more strikingly in experiment B than in experiment A. This suggests that adults from well-nourished larvae tend to develop their horns more fully than adults from ill-nourished larvae. Eberhard (1980, 1982, 1987) points out that untransformed measurements of horn and body sizes show a zigzag relationship (2 discontinuous regression lines) in some species of horned beetles. In my study, however, the untransformed values of horn and body lengths did not show such a clear zig-zag relationship. Past field data on this beetle has not shown such a zig-zag pattern (Siva-Jothy 1987).

On the other hand, the log-log allometric regressions for experiments A and B were clearly discontinuous. In my study, the log-log allometric regressions were effective in demonstrating the discontinuity between the 2 morphs. As mentioned at the beginning of this article, adult size depends on larval size in horned beetles. Therefore, the separation of the allometric regressions suggests that the allometric relationship among adults of this horned beetle is influenced by the quality and quantity of larval food. Except for the work by Emlen (1994, 1996, 1997) and Moczek and Emlen (1998) in scarabeid beetles, no previous studies have experimentally demonstrated such control of a discontinuous allomorphic pattern in horned beetles.

The results of my experiments clearly show that there are 2 morphs in male adults of *A. d. septentrionalis*. The dividing point (horn length, 15 mm) almost agrees with that of the field work of Siva-Jothy (1987). These 2 morphs presumably result from the expression of 2 different sets of genes, and larval nutrition is probably the factor which determines which set of genes will be expressed, thus suggesting that every male carries the necessary genes for both morphs.

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