



## Genetic correlations between weapons, body shape and fighting behaviour in the horned beetle *Gnatocerus cornutus*

Kensuke Okada, Takahisa Miyatake\*

Laboratory of Evolutionary Ecology, Graduate School of Environmental Science, Okayama University

### ARTICLE INFO

#### Article history:

Received 14 September 2008  
Initial acceptance 11 November 2008  
Final acceptance 9 January 2009  
Published online 27 February 2009  
MS. number: 08-00588

#### Keywords:

allometry  
correlated selection  
exaggerated trait  
*Gnatocerus cornutus*  
horned beetle  
pleiotropy  
resource competition

Male fighting frequently results in the evolution of traits used as weapons. Additionally, males with well-developed weapons typically differ behaviourally and morphologically from weaponless males. However, the genetic basis to these phenotypic correlations has not been investigated. The broad-horned flour beetle, *Gnatocerus cornutus*, is a species in which males engage in fights using their enlarged mandibles. We conducted bidirectional selection on beetle mandible length to investigate the correlated responses in male behaviour and body shape. Mandible size diverged significantly after 10 generations of selection. We also found that the microevolutionary enlargement of mandibles affected male morphology and behaviour. Compensatory or supportive traits of the mandibles (head, prothorax, genae and forelegs) also became enlarged, but eye area, antenna, head horn and elytra length were all reduced. These correlated responses in morphology may be the result of developmental integration of these traits and mandibles, but the reduction in size of some traits could also be caused by trade-offs generated by resource competition between characters. In any case, the enlargement of the weapon (mandibles) altered male body shape into a suitable form for fighting. Fighting endurance also evolved as a correlated response to selection on mandible size, with lines selected for larger mandibles able to fight for longer. It therefore appears that morphology and fighting are genetically correlated with each other.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Male–male competition is a key component of sexual selection and can lead to the evolution of exaggerated traits that are used as weapons in male fights (Andersson 1994). Obvious examples include the antlers of deer and the horns and mandibles of beetles (Eberhard 1979; Andersson 1994; Shuster & Wade 2003; Tomkins et al. 2005a). In addition to the actual weapons, traits that support or functionally compensate for the exaggerated character (e.g. neck muscles) are also important in fights (Otte & Stayman 1979; Tomkins et al. 2005b). Thus, males with larger weapons will also possess larger compensatory traits (Otte & Stayman 1979; Tomkins et al. 2005b). The exaggeration of weapons may therefore lead to the enlargement of supportive traits and changes in body shape, towards a morph more suitable for male competition.

In many male beetles, secondary sexual traits such as horns and mandibles have become enlarged over evolutionary time (Thornhill & Alcock 1983; Andersson 1994). Beetle horns and mandibles are weapons when they are used in combat between rival males over access to females (Eberhard 1979; Otte & Stayman 1979; Siva-Jothy 1987; Emlen & Nijhout 2000; Moczek & Emlen 2000; Knell et al.

2004; Tomkins et al. 2005a; Emlen et al. 2007; Okada & Miyatake 2007), and male beetles with larger weapons often also possess a larger head and prothorax (Otte & Stayman 1979; Okada & Miyatake 2004; Tatsuta et al. 2004; Okada et al. 2007). Tomkins et al. (2005b) found a positive phenotypic correlation between the relative sizes of the foretibia and the horns in a dung beetle with a head horn, *Onthophagus taurus*. The traits (head, prothorax and legs) are likely to be supportive of weapons (i.e. they help males carry the enlarged weapons) and important structures in male combat (Otte & Stayman 1979; Tomkins et al. 2005b). Compensatory or supportive traits will be subject to correlational selection, and the variance between weapons and supportive characters will be reduced. As a result, the two traits will become genetically correlated and develop in an integrated manner (Cheverud 1996; West-Eberhard 2003; Klingenberg 2004; Tomkins et al. 2005b). Thus, the exaggeration of weapons leads to the enlargement of these traits and to changes in body shape, to that more suitable for fighting.

In contrast, several recent studies have demonstrated that intraorganism competition between weapons and other traits occurs for resources devoted to somatic structures (Nijhout & Emlen 1998; Tomkins et al. 2005b; Simmons & Emlen 2006; Okada et al. 2008). The resulting morphological trade-offs have usually been restricted to neighbouring body parts (Cowley & Atchley

\* Correspondence: T. Miyatake, Laboratory of Evolutionary Ecology, Graduate School of Environmental Science, Okayama University, Tsushima-naka 111, Okayama 700-8530, Japan.

E-mail address: [miyatake@cc.okayama-u.ac.jp](mailto:miyatake@cc.okayama-u.ac.jp) (T. Miyatake).

1990; Nijhout & Emlen 1998; Emlen 2001) and occur in species developing structures in closed developmental systems, such as in the holometabolous insects (Nijhout & Emlen 1998; Tomkins et al. 2005b; Shingleton et al. 2007). This phenomenon is particularly demonstrated in the trade-offs between horns at the rear of the head and eyes in the dung beetle *Onthophagus acuminatus*, and horns at the front of the head and antennae in *Onthophagus sharpi* (Emlen 2001). These morphological trade-offs have been suggested to play an important role in morphological shaping in the armed beetles (Emlen 2001).

The evolution of weapons is therefore expected to be responsible for body shape in males, especially in fighting forms. Furthermore, changes in body shape caused by weapon enlargement may affect male fighting behaviours, and a number of studies report positive relationships between investment in weapons and fighting frequency (Eberhard 1982; Siva-Jothy 1987; Unrug et al. 2004; Tomkins et al. 2005a; Cook & Bean 2006; Okada & Miyatake 2007; Okada et al. 2007; Reaney et al. 2008). However, although there is a close relationship between the evolution of behaviour and weapons and fighting morphology in males (e.g. Eberhard 1979; Shuster & Wade 2003), no study has demonstrated a genetic relationship between them. Artificial selection experiments that target exaggerated traits directly provide a rich approach for exploring evolutionary variability as the basis of evolution of an exaggerated trait (Wilkinson 1993; Emlen 1996; Nijhout & Emlen 1998; Hosken & Ward 2001; Shingleton et al. 2007).

In the broad-horned flour beetle, *Gnathocerus cornutus*, male beetles fight with their enlarged mandibles (Okada et al. 2006). In addition to the enlarged mandibles, males also develop genae and a pair of small horns on the vertex (a part of the head; Fig. 1), but females lack these completely (Okada et al. 2006). Because *G. cornutus* is easy to rear for many generations, it is easy to select artificially for mandible size (Okada et al. 2006). Thus, this beetle is a good model in which to examine the hypothesis that the exaggeration of weapons is associated with changes in body shape and fighting behaviours. We first investigated the response to bidirectional (up/down) artificial selection for mandible length in experimental populations of *G. cornutus* males. This enabled us to

determine whether mandible length was heritable and to establish populations with different mandible lengths. We subsequently investigated correlated responses in morphological traits and fighting behaviour to our artificial selection on mandible length.

## METHODS

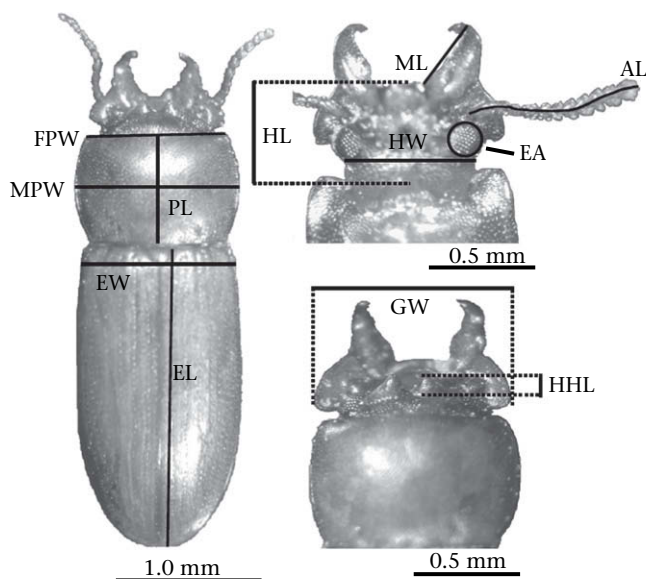
### Beetles

The *G. cornutus* beetle culture has been maintained in the laboratory of the National Food Research Institute, Japan, for 50 years. The culture originated from adults collected in Miyazaki City (31°54', 131°25'), Japan, in June 1957 (Okada et al. 2006). Beetles were reared on whole meal (Yoshikura Shokai, Tokyo, Japan) enriched with brewer's yeast (Asahi Beer, Tokyo, Japan) and kept at 25 °C and 60% relative humidity under a photoperiod of 14:10 h light:dark. To obtain adults for the present experiments, one final-instar larva was placed in each well of a 24-well tissue culture plate (Cellstar; Greiner Bio-One, Frickenhausen, Germany) because pupation in *G. cornutus* is inhibited under high larval density (Okada et al. 2006).

We measured the length of the mandible of each adult ( $\pm 0.01$  mm) with a dissecting microscope monitoring system (Fig. 1; VM-60, Olympus, Tokyo, Japan). Each specimen was carefully positioned so its longitudinal and dorsoventral axes were perpendicular to the visual axes of the microscope eyepiece. Measurements of mandible length were straight-line distances as per Fig. 1.

### Artificial Selection

A random collection of 100 males (10–15 days old) was selected from the stock culture, and their mandibles were measured ( $F_0$  generation). We selected 12 males with the shortest mandibles to propagate short-mandible lines (S lines) and 12 males with the longest mandibles to propagate long-mandible lines (L lines); 12 males were randomly selected to propagate control lines (C line). Body size was not measured when the animals were selected (i.e. we conducted the selection for absolute mandible length). The 12 males of each line were randomly divided into four groups (three males in each), and each group was placed in a plastic cup (7 cm diameter, 2.5 cm height) with 20 g of medium and three females. Females do not have mandibles, so were chosen randomly from the stock culture. Groups were maintained for 2 months with males able to mate with females and females were allowed to lay eggs in each group, until final-instar larvae were obtained. Each male and female within the group was equally likely to contribute to the next generation because we observed the females copulating with two or more males (K. Okada, unpublished data) and the males had enough time (i.e. 2 months) to copulate with all females. Final-instar larvae were collected to obtain the adults for subsequent generations. Briefly, one final-instar larva was placed in each well of a 24-well tissue culture plate. When the adults reached 10–15 days old, we randomly collected 100 males from each line and measured their mandible length ( $F_1$  generation). The same selection regimes for each line were continued for 10 generations, that is, 12 males were selected from each line for the next generation. Females were chosen randomly from within each line. Two selection replicates with two populations from the stock culture for the short, long and control lines (L1, C1 and S1; L2, C2 and S2) initiated at the same time were tested and maintained in the chamber. Realized heritability was calculated as described by Falconer & Mackay (1996). At generation 10 of S, C and L lines, male adults were used for the following experiments.



**Figure 1.** Morphological measures made on male *G. cornutus*. ML: mandible length; FPW: foreprothorax width; MPW: midprothorax width; PL: prothorax length; EW: elytra width; EL: elytra length; HL: head length; HW: head width; GW: genae width; HHL: head horn length; AL: antenna length; EA: eye area.

Download English Version:

<https://daneshyari.com/en/article/2417619>

Download Persian Version:

<https://daneshyari.com/article/2417619>

[Daneshyari.com](https://daneshyari.com)