

Morphological patterns of sexual selection in the diving beetle *Graphoderus liberus*

Albrecht Schulte-Hostedde* and Yves Alarie

Department of Biology, Laurentian University, Sudbury,
Ontario P3E 2C6, Canada

ABSTRACT

Hypotheses: Individuals in good condition are better able to invest in costly traits associated with sexual selection and sexual conflict than individuals in poor condition. Sexual selection favours males with male genitalia that are appropriate for stimulating any encountered female ('one size fits all' hypothesis) and thus the allometric slopes of genitalia should be equal to 0.

Organism: The diving beetle *Graphoderus liberus*.

Time and place: July 2004; Swan Lake near Sudbury, Ontario, Canada.

Analytical methods: Multivariate analysis to identify dimorphic traits. Analysis of body condition (via size-corrected mass) and correlations with dimorphic traits and genitalia. Allometric analyses of size of male genitalia.

Traits studied: Protarsal pads and pronotum (male traits used for grasping females when copulating).

Results: Females tended to be larger than males but males had larger pronota. Both the area of the male protarsal pad and pronotum length were proportional to the condition of the individual. Female pronotum length did not depend on the condition of the individual. The length and width of male genitalia did not depend on condition, and their allometric slopes did not differ significantly from zero.

Conclusion: Traits associated with sexual selection and sexual conflict conformed to sexual selection theory. Males in better condition have larger structures for grasping females when copulating. In contrast, male genitalia conform to the 'one size fits all' hypothesis.

Keywords: allometry, condition dependence, genitalia, insects.

INTRODUCTION

Sexual dimorphism is the result of independent, sex-specific selection acting on morphological traits (Price, 1984; Greenwood and Adams, 1987; Hedrick and Temeles, 1989; Andersson, 1994; Blanckenhorn, 2000). Sexual selection is a potent force often leading to the evolution of these sex differences in morphology (Andersson, 1994). In particular, sexual selection acting on traits

* Author to whom all correspondence should be addressed. e-mail: aschultehostedde@laurentian.ca
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such as ornaments for attracting mates or traits associated with male–male competition, such as combat, often results in the evolution of large body size, colourful traits, and/or weapons in males, whereas females tend to be small, drab, and without weaponry (Andersson, 1994).

Sexual selection theory predicts that traits associated with male–male competition or female mate choice must be costly and heritable to confer an evolutionary advantage to those individuals carrying such traits (Andersson, 1994; but see Bonduriansky and Rowe, 2005). Thus, males that are capable of bearing the costs of expensive traits are likely to be more successful at male–male competition or at attracting females. This hypothesis predicts that sexually selected traits should depend on the physiological condition of the individual. The hypothesis is particularly important in good-genes models of sexual selection (Andersson, 1994). Evidence is accumulating that structures associated with male–male combat (Côté and Festa-Bianchet, 2001; Festa-Bianchet *et al.*, 2004; Bonduriansky and Rowe, 2005) and female mate choice (Keyser and Hill, 1999; Møller and Petrie, 2002; Cotton *et al.*, 2004) are condition-dependent. Traits related to mating behaviour have also been found to be related to body condition (Kotiaho, 2000). Dimorphic traits should also show heightened condition dependence in males compared to the homologous trait in females because sexual selection is presumed not to act on female traits (e.g. Cotton *et al.*, 2004). These models and empirical tests are based on the assumption that body condition is heritable (e.g. Merilä *et al.*, 2001; Simmons and Kotiaho, 2002; Houle and Kondrashov, 2002).

Because of their morphological diversity, male genitalia, especially those of insects, offer a unique structure to test sexual selection theory (Hosken and Stockley, 2004). Not only should genitalia under sexual selection be condition dependent, but hypotheses regarding the allometric relations of genitalia have been proposed. Two hypotheses (the ‘good viability genes’ hypothesis and the ‘weapons’ hypothesis) predict that the genitalia should be disproportionately larger in large males than in small males, and that allometric relations for genitalia should be higher than other body parts governed by selection pressures similar to overall body size (Eberhard *et al.*, 1998). However, recent evidence suggests that the allometric slopes of genitalia are lower than those of other body parts, giving rise to the ‘one size fits all’ hypothesis (Eberhard *et al.*, 1998; Bernstein and Bernstein, 2002), which suggests that sexual selection favours males with genitalia appropriate to stimulate any female encountered during the mating season (Eberhard *et al.*, 1998). This pattern of negative allometry has been found both in vertebrate (Kelly *et al.*, 2000; Miller and Burton, 2001; but see Jennions and Kelly, 2002) and invertebrate taxa (e.g. Eberhard *et al.*, 1998; Tatsuta *et al.*, 2001).

The diving beetles (Coleoptera: Dytiscidae) are a large group of aquatic predatory beetles with streamlined bodies and a worldwide distribution (Larson *et al.*, 2000). During mating, the male beetle attacks the female from behind and grasps her with large and small suction discs that appear on the three basal segments of his protarsi and sometimes mesotarsi (Aiken and Khan, 1992; Bergsten *et al.*, 2001). There is no courtship and females often struggle to resist male mating attempts by diving and/or swimming quickly and erratically (Aiken, 1992; Aiken and Khan, 1992). Because of the presence of male discs and female structural modifications on the elytral surface upon which the males attach themselves, this mating system has been examined in the context of sexual conflict and antagonistic co-evolution (Bergsten *et al.*, 2001; Miller, 2003). Thus, although these structures are not associated with male–male combat or female choice *per se*, they are nonetheless required for the acquisition of copulations and as such should be under sexual selection.

Here we use the diving beetle *Graphoderus liberus* (Say) to examine several issues related to sexual selection of morphological traits. First, we use univariate and multivariate

techniques to identify sexually dimorphic structures. Second, we test the prediction that sexually dimorphic structures associated with male mating success, including the genitalia, are condition-dependent. Finally, we focus on the genitalia, and test the prediction of the 'one size fits all' hypothesis that the allometric slopes of the length and width of the male genitalia (the aedeagus) are lower than those of other body parts (Eberhard *et al.*, 1998; Bernstein and Bernstein, 2002).

METHODS

Study species

Graphoderus liberus is found in boggy (often brown-water) ponds and lakes (Larson *et al.*, 2000). The specimens studied were collected near Sudbury, Ontario, Canada in Swan Lake, a small (6 ha surface area, 8.5 m maximum depth) lake without fish, historically acidified by local sulphur deposition. Collecting was done over several days during the breeding season (early June 2004) (Y. Alarie, personal observation) to ensure that beetles were of the same physiological age. Sampling was done using D-net sweeps on a variety of microhabitats, including macrophyte beds, rocky shores, and organic-rich sediment. Collected specimens were kept alive and transported to the laboratory for measurements (see below). To prevent injuries, we did not overcrowd the beetles in the collection containers.

Measurements

Upon arrival at the laboratory, individual beetles were sexed, weighed (± 0.001 g), placed in a marked vial, and preserved in a 70% ethanol solution. Each specimen was blotted with a paper towel to remove excess water when mass was measured.

Measurements were made using an Olympus SZH10 research stereo microscope equipped with a micrometer eyepiece. The trait to be measured was adjusted so that it was, as nearly as possible, parallel to the plane of the objective lens. The characters and terms used in the morphometric analysis are defined as follows:

- *Total head length* (HL): measured dorsally along the mid-line.
- *Pronotum length* (PL): measured dorsally along the mid-line.
- *Elytral length* (EL): measured dorsally along the mid-line.
- *Standardized body length* (SBL): obtained from the sum of three measurements, HL, PL, and EL [the use of SBL avoids error due to variation in extension or retraction of body parts among specimens (Alarie, 1993)].
- *Body width* (BW): greatest transverse width measured dorsally.
- *Body height* (BH): greatest dorsal-ventral depth of the body measured between the procoxae and mesocoxae.

The following structures occur on males only:

- *Length and width of protarsal pads*: male *G. liberus* are characterized by the presence of enlarged tarsomeres (i.e. tarsal pads) on the prothoracic legs; protarsal pads are made of three articles or tarsomeres (= AR1, AR2, and AR3). We measured length (greatest linear distance measured along the mid-line) and width (greatest transverse distance

measured transversally) of each protarsal pad on both legs (i.e. left AR1 length, left AR1 width, right AR1 length, right AR1 width, etc.)

- *Number of suction discs on protarsal pads*: the ventral surface of the protarsal pads is characterized by the presence of ventral adhesion cupules or suction discs. Suction discs were counted on each protarsal pad.
- *Length of aedeagus (AEL)*: the male genitalia consists of three lobes, a median aedeagus and lateral parameres. The length of the aedeagus is the longest linear distance between the two most extreme ends. We measured the AEL of 50 males subsampled from the original sample of 144 individuals.

Statistical analysis

For each body size component measured in both sexes, dimorphism ratios were calculated by dividing the mean female component by the mean male component. Independent *t*-tests on \log_{10} -transformed data were performed to compare the seven homologous body-size components between male and female water beetles. All subsequent analyses were based on \log_{10} -transformed data and the data conformed to a normal distribution unless noted.

We determined whether discriminant function analysis (DFA) could distinguish between males and females based on five log-transformed body-size components. The discriminant function analysis first used a multivariate analysis of variance (MANOVA) to establish a significant difference among groups (Pimentel, 1979) and then classified each individual to the sex it most resembled, calculated the Mahalanobis distances between the group centroids, and calculated a canonical vector that maximized the variation in the body-size components in discriminant space (analogous to a principal components analysis) (Pimentel, 1979).

Traits analysed for condition-dependence were sexually dimorphic – either larger in males than females, or present only in males. These traits were pronotum length, the area (three articles or tarsomeres) of the left prothoracic leg associated with the discs of the male (protarsal pad), the number of discs associated with the protarsal pads of the left protarsus, and the length and width of the aedeagus. The area of the prothoracic leg associated with the discs was estimated by calculating the area of each of the three tarsomeres (length \times width) because tarsomeres are roughly rectangular.

To examine condition dependence of dimorphic traits and traits associated with mating in males (area of the protarsal pad, number of discs, pronotum length, length and width of aedeagus), we used a multiple regression incorporating elytral length (as a measure of structural size) and body mass as independent variables. We selected elytral length as a measure of overall size because the elytron is a large, flat structure than can be measured accurately and precisely (Bernstein and Bernstein, 2002). We interpreted the partial correlation coefficient of body mass as ‘body condition’ because it represents the effects of mass on the dependent variable, after controlling for body size (elytron length) (e.g. Schulte-Hostedde and Millar, 2004; Schulte-Hostedde *et al.*, 2005). We assumed that size-corrected mass reflected energy reserves. For example, there was a significant positive correlation between residual mass and fat reserves in the carabid beetle *Pterostichus melanarius* (Oestman *et al.*, 2001). Allometric relationships were determined by calculating the slope between elytral length and the genitalia.

RESULTS

Sexual size dimorphism

Female water beetles ($n = 114$) were generally larger than males ($n = 144$), both with respect to body mass and standard body length (Table 1). In all but one morphological trait, females were consistently larger than males. Interestingly, despite this pattern, males had a longer pronotum than females.

The initial multivariate analysis of variance (MANOVA) indicated a significant difference between the sexes in overall size (Mahalanobis distance = 2.111, Wilks' $\lambda = 0.656$; $F_{5,252} = 26.44$, $P < 0.001$). The discriminant function analysis correctly assigned 79.07% of individuals (83.33% of males and 73.68% of females), indicating that the five morphological traits could be used to discriminate between the sexes. Four of the five morphological variables were positively correlated with the canonical vector. Only pronotum length was negatively correlated (Table 2). The mean canonical score for males was -0.642 , whereas that for females was 0.811 (Fig. 1).

Table 1. Mean values (\pm standard deviations) and dimorphism ratios (female/male) of measured traits for male and female water beetles, together with the results of independent t -tests

Trait	Females	Males	Dimorphism ratio	t -value	P -value
Head length (mm)	1.70 \pm 0.147	1.62 \pm 0.177	1.043	3.71	<0.001
Pronotum length (mm)	1.68 \pm 0.077	1.72 \pm 0.100	0.978	-3.07	0.002
Elytral length (mm)	9.74 \pm 0.409	9.48 \pm 0.413	1.028	5.20	<0.001
Body length (mm)	13.13 \pm 0.450	12.82 \pm 0.433	1.024	5.53	<0.001
Body width (mm)	7.09 \pm 0.224	6.90 \pm 0.245	1.028	6.52	<0.001
Body height (mm)	4.05 \pm 0.156	3.90 \pm 0.133	1.038	8.07	<0.001
Body mass (g)	0.140 \pm 0.010	0.123 \pm 0.008	1.138	14.54	<0.001
Aedeagus length (mm)	—	1.61 \pm 0.078	—	—	—
Aedeagus width (mm)	—	0.579 \pm 0.050	—	—	—
Protarsal discs (n)	—	20.72 \pm 0.72	—	—	—
Area of protarsal pad (mm ²)	—	0.865 \pm 0.09	—	—	—

Note: Sample sizes are provided in the text.

Table 2. Factor structure of canonical vector for five body-size components of the water beetle

Morphological trait	Factor structure
Head length	0.327
Pronotum length	-0.267
Elytral length	0.447
Body width	0.560
Body height	0.696

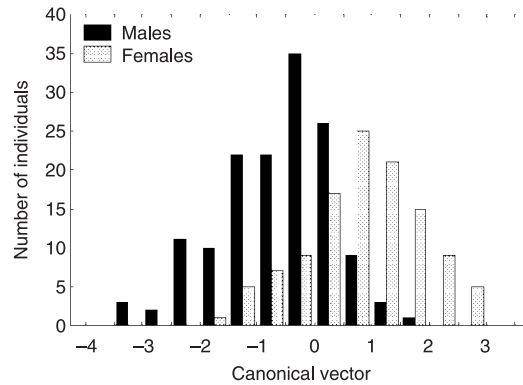


Fig. 1. Frequency distribution of canonical discriminant scores for male and female water beetles. The mean canonical scores are -0.642 for males and 0.811 for females.

Condition dependence of dimorphic traits

Sexual selection theory predicts that traits under sexual selection should be condition-dependent. In addition, homologous traits in females are not expected to be condition-dependent. We identified the pronotum (present in both sexes), the protarsal pad, the number of protarsal discs, and the length and width of the aedeagus as traits likely to be under sexual selection. Consistent with the prediction of condition dependence, males in good condition had significantly larger pronota ($F_{2,141} = 9.21$, $r^2 = 0.115$, $P < 0.001$; body mass partial $r = 0.266$, $P = 0.001$) (Fig. 2) than males in poor condition, whereas the pronota of female beetles were not condition-dependent ($F_{2,112} = 1.78$, $r^2 = 0.03$, $P = 0.17$; body mass partial $r = 0.17$, $P = 0.07$). In addition, the left protarsal pad of males in good condition had a larger area than the pad of males in poor condition ($F_{2,141} = 14.04$, $r^2 = 0.155$, $P < 0.001$; body mass partial $r = 0.376$, $P < 0.001$) (Fig. 3).

Counter to our predictions from sexual selection theory, the number of protarsal discs and the length and width of the aedeagus were not condition-dependent. The number of discs on the protarsus was not normally distributed (Kolmogorov-Smirnov test: $d = 0.46$, $P < 0.01$), thus to determine if the number of discs was related to body condition we conducted a rank correlation between residual mass (residuals from the regression of body mass on elytral length) and the number of discs. We found no evidence of condition dependence of the number of discs ($r_s = -0.05$, $P = 0.51$). We also found no evidence that the length or width of the aedeagus was related to body condition (length: $F_{2,47} = 1.07$, $r^2 = 0.04$, $P = 0.35$; body mass partial $r = 0.194$, $P = 0.18$; width: $F_{2,47} = 0.81$, $r^2 = 0.03$, $P = 0.81$; body mass partial $r = -0.18$, $P = 0.22$).

Allometry of male genitalia

The 'one size fits all' hypothesis predicts that the male genitalia have an allometric slope that is less than that of other traits, and indeed the allometric slope may not differ from zero (Eberhard *et al.*, 1998, Bernstein and Bernstein, 2002). We found no evidence that the length or width of the aedeagus increased with size; neither slope estimate was significantly different from zero [length $B = 0.062 \pm 0.12$ (standard error), $r^2 = 0.006$, $P = 0.59$; width $B = 0.061 \pm 0.22$, $r^2 = 0.002$, $P = 0.78$]. The absence of a correlation contrasted with the allometric slopes

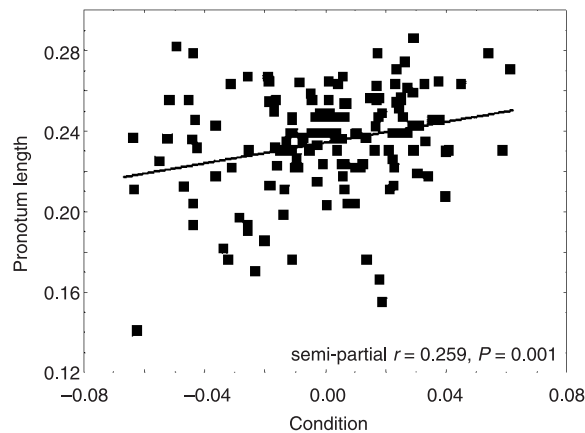


Fig. 2. Semi-partial correlation between pronotum length and residual body mass (corrected for elytral length) for male water beetles ($n = 144$) (all variables are log-transformed). Males in good condition had larger pronota than males in poor condition.

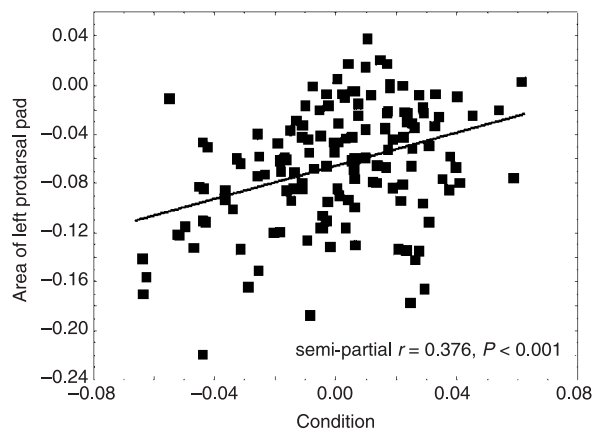


Fig. 3. Semi-partial correlation between total area of the left protarsal pad and residual body mass (corrected for elytral length) for male water beetles ($n = 144$) (all variables are log-transformed). Males in good condition had a larger pad than males in poor condition.

of other structures, which were significantly different from zero, including the pronotum ($B = 0.304 \pm 0.113$, $r^2 = 0.048$) and body width ($B = 0.192 \pm 0.067$, $r^2 = 0.054$, $P = 0.005$).

DISCUSSION

The initial analysis of morphology indicated that females were larger than males in overall size, yet males had larger pronota than females. The pronotum and the area of the protarsal pad conformed to sexual selection theory, as both traits were condition-dependent. Males in good condition had larger pronota and protarsal pads than males in poor condition. In addition, the female pronotum was not condition-dependent, lending support to the idea that the male pronotum represents a sexually selected trait. The results also indicate that the

genitalia do not conform to sexual selection theory. First, neither the length nor width of the aedeagus was condition-dependent. Second, the allometric relations were not indicative of sexual selection, and indeed the lack of relationship between elytral length and genital size is consistent with the 'one size fits all' hypothesis proposed by Eberhard *et al.* (1998).

Condition dependence of traits associated with combat and mate choice have been related to body condition in other species of insects, usually using a manipulative laboratory experiment. Males of the fly *Prochyliza xanthostoma* that were fed a high-quality diet had longer heads (used for both courtship and male–male combat) than males on a poor-quality diet (Bonduriansky and Rowe, 2005). Similar patterns have been found in the eye-span of stalk-eyed flies (*Cyrtodiopsis dalmanni*). Males raised on a high-quality diet (good condition) had wider eye-spans than males on a poor-quality diet (poor condition) (Cotton *et al.*, 2004). In addition, females in good condition did not show an increase in eye-span width relative to females in poor condition (Cotton *et al.*, 2004). Thus there is substantial evidence that sexually selected traits do depend on individual condition and that if that condition is heritable, a female can gain genetic benefits because she can confer the genes associated with good condition to her offspring (Merilä *et al.*, 2001; Simmons and Kotiaho, 2002). Our results suggest that a field test might also detect condition dependence of morphological traits.

The dimorphic traits of male *G. liberus* are not associated with male–male combat, nor are they ornaments for attracting females as in other examples of condition dependence. The mating system of the Dytiscidae is characterized by the males grasping the female from behind using the discs on their protarsal pads to attach to the elytron of the female (Aiken, 1992; Aiken and Khan, 1992; Bergsten *et al.*, 2001). The female resists the mating attempt by diving and swimming quickly and erratically (Aiken, 1992; Aiken and Khan, 1992; Bergsten *et al.*, 2001). The protarsal pads and associated discs are clearly an adaptation for grasping the female and an enlarged pronotum is also important because it serves as the surface upon which the leg muscles of the protarsi are attached. These morphological patterns are consistent with intra-locus sexual conflict, in which the fitness optima for a trait are different for males and females (Chapman *et al.*, 2003). Males in good condition may be able to overcome the resistance offered by females by developing larger protarsal pads and larger pronota (Chapman *et al.*, 2003). An alternative interpretation is that female resistance to copulatory attempts by males may function to 'screen' males of variable genetic quality so that only males of good quality are able to overcome female resistance (Cordero and Eberhard, 2003). Because the structures associated with copulation in males are condition-dependent, males in good condition can produce protarsal pads and pronota that likely enhance the probability of successful copulation. Thus females that cannot resist the copulatory attempts of a male may be acquiring a mate of high quality (i.e. good condition).

The evolution of genital size and shape has recently been debated with sexual selection being targeted as the likely source of the tremendous variation evident among male genital morphology (Hosken and Stockley, 2004). Despite this recent emphasis on sexual selection, we found no evidence that male genitalia in *G. liberus* were condition-dependent or conformed to allometric relations consistent with the 'good genes' or 'weapons' sexual selection hypotheses (Eberhard *et al.*, 1998). Indeed, our results are in line with other tests of these hypotheses in other insects and arachnids. Eberhard (2002) found that allometric slopes in male genitalia were consistently lower than slopes associated with other body parts for 20 species of insects and spiders. Bernstein and Bernstein (2002) found this pattern in *Chauliognathus scutellaris*, a species of soldier beetle, as did Tatsuta *et al.* (2001) in the stag

beetle, *Lucanus maculifemoratus*. In contrast, other studies have found that male genital morphology is related to mating success (Arnqvist and Danielsson, 1999; House and Simmons, 2002), indicating that further study is needed to elucidate broad patterns. One possibility is that specific structures associated with all or part of the genitalia may be used by the female to assess male quality rather than overall genital size (see Arnqvist and Danielsson, 1999; House and Simmons, 2002). Thus detailed measurements of the components of male genitalia and determining their relationship with mating success will be needed to ascertain the role of sexual selection on specific components of the male genitalia.

Our results offer several intriguing directions for further study using *G. liberus* as a model. First, we predict that males with larger protarsal pads and larger pronota will have higher mating success than males with small structures. Second, further examination of condition dependence of dimorphic structures, such as the pronotum and the protarsal pads, and the heritability of condition will require an experimental approach *sensu* Bonduriansky and Rowe (2005). Finally, although we did not find that male genitalia size was consistent with sexual selection hypotheses, further examination of specific structures is warranted. For example, do males with larger aedeagi have higher mating or fertilization success? Are specific components of the aedeagus governed by sexual selection? *Graphoderus liberus* may be an ideal model to test hypotheses in sexual selection and sexual conflict.

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