

**SEXUAL SIZE AND SHAPE DIMORPHISM IN *DINEUTUS NIGRIOR*
(COLEOPTERA: GYRINIDAE)**

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Abstract

Sexual size and shape dimorphism was quantified in the whirligig beetle *Dineutus nigrior* Roberts. Females were larger in terms of body length, elytra length, body height, profemur width, and mass. Males had longer heads, longer and wider protarsi, longer and wider protibiae, and longer profemora. Discriminant function analysis identified 80.5% of individuals as the correct sex based on measurements of body size. Males and females also differed in terms of body shape. Potential causes of the dimorphism are discussed.

All sexually reproducing species are inherently sexually dimorphic. The sexual difference in external morphology, however, ranges from totally indistinguishable (*i.e.*, inconspicuously dimorphic) to enormous in size and shape (*i.e.*, conspicuously dimorphic) with all degrees and types of intermediates in beetle (Coleoptera) species (Kawano 2006).

Sexual dimorphism is caused by independent, sex-specific selection on morphological traits (Price 1984; Greenwood and Adams 1987; Andersson 1994; Blanckenhorn 2000). Several hypotheses have been proposed to explain the different selection pressures on the sexes in dimorphic species including sexual selection, fecundity selection, and ecological niche divergence. Sexual selection is often thought to be the cause of larger body size in males due to larger males having an advantage in male-male competition (Andersson 1994; Weckerly 1998). In addition to acting on overall body size, sexual selection can favor larger size in particular morphological traits if more extreme development of a trait confers a mating advantage mainly on individuals in one sex (Andersson 1994). Sexual selection is generally stronger on males than females (Andersson 1994) and is often the cause of male-biased trait dimorphism in insects (*e.g.*, Tseng and Rowe 1999; Teder 2005). Increased fecundity in large females is generally thought to be the cause of larger body size (Honek 1993; Andersson 1994; Blanckenhorn 2000). Female biased size dimorphism is the more common pattern of sexual size dimorphism in animals, especially invertebrates (Teder and Tammaru 2005). However, there are arthropod species in which males are the larger sex (*e.g.*, Wiklund and Forsberg 1991; Juliano 1992). Ecological niche divergence between the sexes occurs in some animal species. When the optimal morphology is different for the different niches sexual dimorphism can result (Slatkin 1984; Shine 1989).

Explaining the evolution and maintenance of sexual size dimorphism first requires measuring and quantifying dimorphism to prove that sexual size dimorphism is present. Here we use univariate and multivariate methods to quantify previously undescribed sexual size and shape dimorphism in body size in a natural population of the whirligig beetle (Gyrinidae) *Dineutus nigrior* Roberts

which is commonly found at the water surface of lakes. Although sexual dimorphism in body size has not been described in *D. nigrior*, there is conspicuous male-biased dimorphism in the protarsus. However, the magnitude of this dimorphism has not been quantified for this species. In addition to describing size and shape dimorphism in body size, we quantify the sexual size dimorphism in the protarsus and determine if sexual dimorphism is also present in other prothoracic leg traits.

Methods

Measurements. A total of 426 adult beetles (363 females, 63 males) were collected from Swan Lake, a small (6 ha surface area, 8.5 m maximum depth), fishless lake near Sudbury Ontario, Canada, historically acidified by local sulphur deposition. All beetles were collected during the breeding season of 2004. Nets were used to opportunistically sample beetles that were observed swimming on the water surface. Collected beetles were transported alive to the laboratory. To prevent injuries to the beetles during transportation the transportation containers were not overcrowded. All collected beetles were sexed and weighed (± 0.001 g), then preserved in marked vials containing 70% ethanol. Excess water was blotted from each specimen with paper towel immediately before mass was measured.

Linear measurements were obtained using a micrometer-equipped Olympus SZH10 research stereo microscope. Before each trait was measured, the specimen was oriented so that the trait of interest was as close to parallel to the plane of the objective lens as possible. Measurements of aspects of body size were performed on all specimens (with the exception of head length and mass of one female). Measurements of components of the prothoracic leg were performed on a random sub-sample of 30 females and 29 males.

The body size traits used are as follows:

Head length (HL): measured dorsally along mid-line

Pronotum length (PL): measured dorsally along mid-line

Elytra length (EL): measured dorsally along mid-line

Standardized Body length (SBL): sum of HL, PL, and EL; avoids error caused by differences in retraction or extension of body parts (Alarie 1993).

Body width (BW): maximum transverse width measured dorsally

Body height (BH): maximum dorso-ventral depth measured between pro- and mesocoxae.

The prothoracic leg traits used are as follows:

Profemur length (PFL): measured along anterior margin

Profemur width (PFW): measured at greatest transverse width

Protibia length (PTiL): measured along anterior margin

Protibia width (PTiW): measured at distal margin

Protarsus length (PTaL) and width (PTaW): The protarsus is comprised of five tarsomeres; length (greatest linear distance measured along mid-line) and width (greatest transverse distance measured transversally) of each tarsomere were measured on the right prothoracic leg. Protarsus length was determined by adding the lengths of the five tarsomeres. Protarsus width was determined by finding the average width of the five tarsomeres.

Statistical Analysis. All variables were \log_{10} -transformed to improve normality. We tested for dimorphism in absolute trait size using independent *t*-tests. Dimorphism ratios were calculated by dividing the mean female measurement by the mean male measurement. The means were back transformed from the mean of the \log_{10} -transformed data.

Discriminant function analysis (DFA) was performed to determine if five body size variables (HL, PL, EL, BW, BH) could be used to distinguish between males and females. The DFA first established if there was a difference between the groups using a multivariate analysis of variance (MANOVA). It then classified each individual to the sex it most resembles, calculated the Mahalanobis' distances between group centroids, and calculated a canonical vector that maximized the variation in the body size components in discriminant space (analogous to a principle components analysis) (Pimentel 1979).

To determine if the sexes differed in terms of body shape we used ANCOVA with a body size trait (HL, PL, EL, BW, or BH) as the dependent variable, sex as a factor, and SBL as a covariate.

Results

Sexual size dimorphism was present in the study population. Females were significantly larger than males in terms of mass, elytra length, standardized body length, body height, and profemur width. Males had longer heads, longer and wider protibiae and protarsi, and longer profemora (Table 1).

MANOVA showed a significant difference between the sexes in terms of structural body size (Wilks lambda = 0.745, $F_{(5,419)} = 28.735$, $P < 0.001$). The squared Mahalanobis distance between male and female centroids was 2.703 ($P < 0.001$). The DFA was able to identify 80.47% of the specimens as the correct sex (81.22% of females, 76.19% of males). Pronotum length and head length were negatively correlated with the canonical vector and elytra length, body width and body height were positively correlated with the canonical vector (Table 2). The mean canonical score for males was -1.400, and 0.244 for females. The distribution of canonical scores is presented in Fig. 1.

Body shape dimorphism was also present in *D. nigrior*. The slopes of trait vs. standardized body length did not differ between the sexes in any case (homogeneity of slopes ANCOVA, $P > 0.299$) therefore determining differences between the elevation of the slopes using ANCOVA was appropriate. When body size was controlled for males had significantly longer heads ($F_{(1, 421)} = 22.62$; $P < 0.001$; Fig. 2a) and longer pronota ($F_{(1, 422)} = 8.81$; $P = 0.003$; Fig 2b) and there was a trend towards wider bodies in males when SBL was controlled for ($F_{(1, 422)} = 3.34$; $P = 0.068$, Fig. 2d). Females had longer elytra ($F_{(1, 422)} = 46.79$; $P < 0.001$; Fig. 2c) and deeper bodies ($F_{(1, 422)} = 56.92$; $P < 0.001$, Fig. 2e) when SBL was controlled for.

Discussion

Most beetle species are inconspicuously dimorphic where the male and female can be distinguished only by minor (often microscopic) morphological difference (Kawano 2006). As shown in this study, sexual size dimorphism is present in *D. nigrior*. Females were found to be significantly larger than males in terms of mass, EL, SBL, BH, and PFW. Females are typically larger than males in animals, especially invertebrates (Teder and Tammaru 2005), and an increase in fecundity (through increased egg production) in females with larger body size is often thought to be the cause of this pattern (Andersson 1994). Fecundity selection is a likely cause of the body size dimorphism in *D. nigrior* as generally the traits that were female biased represented the area where eggs are produced and stored (EL, BH).

Head length was significantly larger in males than females. Although intersexual selection is potentially responsible for longer head length in males it does not seem

Table 1. Means (± 2 SE) and dimorphism ratios for morphological traits of male and female *Dineutus nigror*. Means are back transformed from \log_{10} transformed data and ± 2 SE intervals are asymmetrical around the mean because of back transformation. The results of independent *t*-tests for differences between the sexes are also provided. Units for all traits are mm, except g for body mass.

Trait	Female		Male		Dimorphism ratio	<i>t</i> -value	P
	n	Mean (± 2 SE)	n	Mean (± 2 SE)			
Head length	362	2.22 (2.20-2.23)	63	2.27 (2.23-2.31)	0.978	-2.40	0.017
Pronotum length	363	1.92 (1.90-1.93)	63	1.93 (1.89-1.96)	0.995	-0.422	0.673
Elytra length	363	8.31 (8.27-8.34)	63	8.00 (7.91-8.09)	1.039	6.41	<0.001
Body length	362	12.45 (12.39-12.49)	63	12.20 (12.07-12.32)	1.020	3.66	<0.001
Body width	363	6.44 (6.42-6.47)	63	6.43 (6.36-6.50)	1.002	0.318	0.750
Body height	363	3.68 (3.67-3.70)	63	3.50 (3.46-3.53)	1.051	9.17	<0.001
Body mass	362	0.084 (0.083-0.084)	63	0.081 (0.079-0.083)	1.037	2.49	0.013
Protarsus length	30	1.16 (1.14-1.18)	29	1.29 (1.26-1.31)	0.899	-7.38	<0.001
Protarsus width	30	0.193 (0.189-0.196)	29	0.340 (0.332-0.347)	0.568	-39.5	<0.001
Profemur length	30	2.77 (2.74-2.80)	29	2.85 (2.81-2.90)	0.972	-2.97	0.004
Profemur width	30	0.643 (0.633-0.653)	29	0.625 (0.615-0.635)	1.029	2.50	0.015
Protibia length	30	2.16 (2.14-2.19)	29	2.22 (2.19-2.25)	0.973	-2.64	0.011
Protibia width	30	0.350 (0.343-0.357)	29	0.491 (0.482-0.500)	0.713	-24.22	<0.001

Table 2. Factor structure of canonical vector for five body size components of *Dineutus nigrrior*.

Trait	Canonical structure
Head length	-0.167
Pronotum length	-0.033
Elytra length	0.533
Body width	0.030
Body height	0.713

likely as there is no obvious courtship or female mate choice in this species. Males simply attempt to grasp the female from behind with the enlarged tarsi and females resist by swimming away (Y. Alarie, pers. obs.). Females may use the resistance as a method of “screening” potential mates ensuring that only males of good quality are able to overcome the resistance (Cordero and Eberhard 2003) but it does not seem likely that this form of mate choice would favor longer heads.

Intrasexual selection may also lead to male-biased dimorphism. Traits used as weapons in male-male combat are sexually selected and often male-biased (Andersson 1994). In *D. nigrrior* there may be male-male combat for control of prime oviposition sites (Fitzgerald 1987). Several territorial behaviors are exhibited including an “attack” where two individuals wrestle using the front legs and mouthparts (Fitzgerald 1987). A larger head may be advantageous in this type of competition, possibly by allowing for greater musculature to support larger and stronger mouthparts. Alternatively to sexual selection, the dimorphism

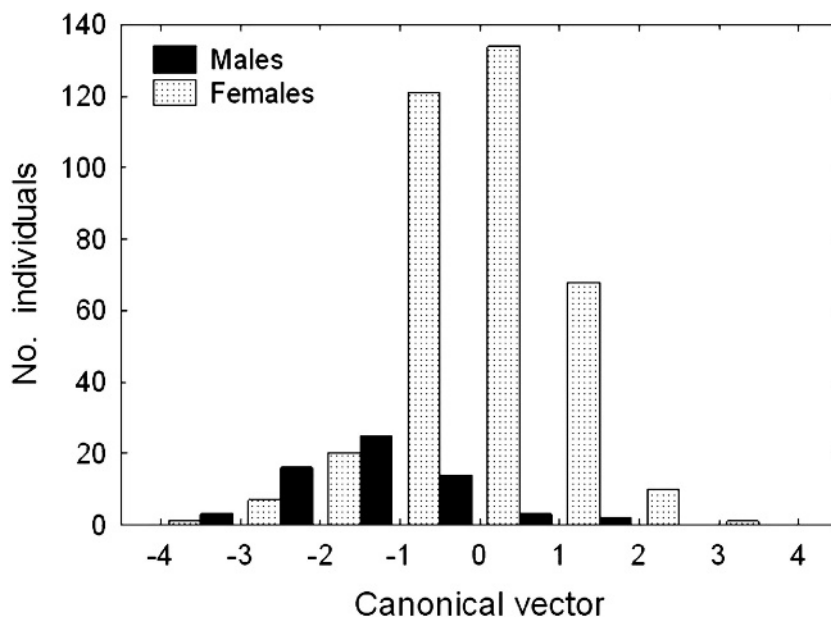


Fig. 1. Frequency distribution of canonical discriminant scores for male and female *Dineutus nigrrior*.

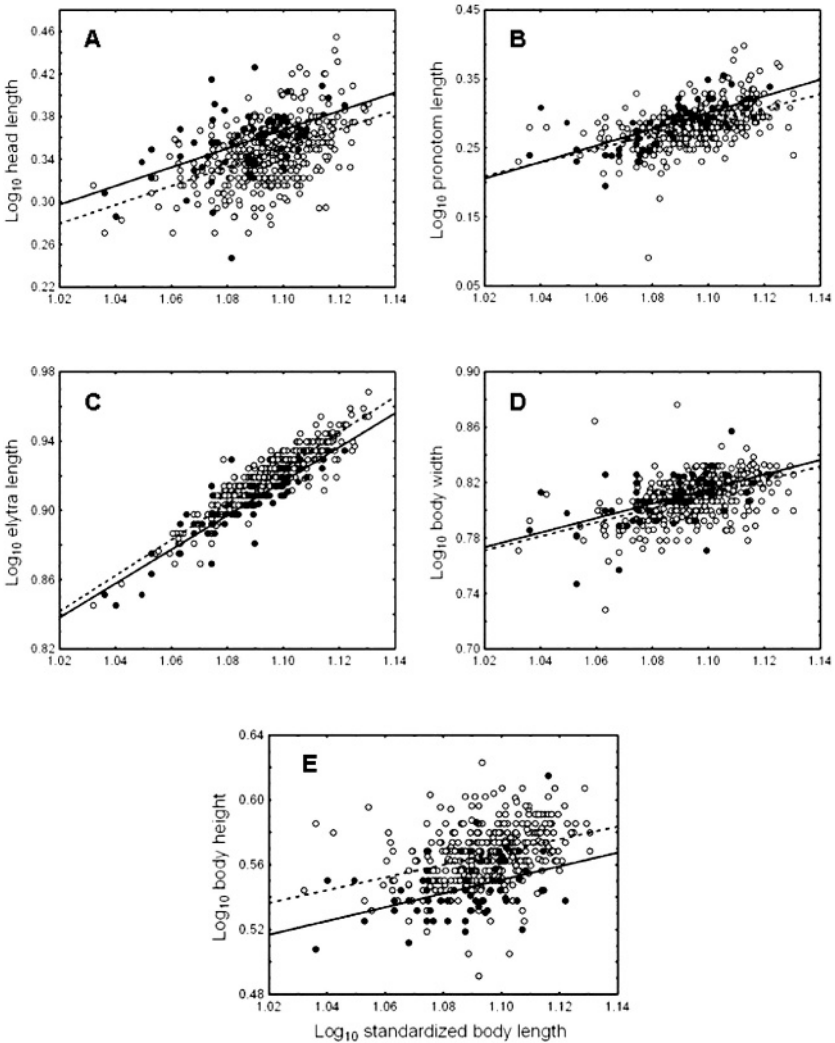


Fig. 2. Relationships between standardized body length and other body size measures in male and female *Dineutus nigrior*. Filled circles and solid lines indicate males; open circles and broken lines indicate females. Male $n = 63$, female $n = 362-363$.

in head length could be caused by feeding niche divergence between the sexes (Selander 1966; Nudds and Kaminski 1984; Shine 1989; Temeles *et al.* 2000). Gyrinids feed largely on invertebrates on the water surface. To decrease intersexual competition for food items males may have evolved to consume larger food items resulting in a longer head to increase the gape size or size of mouthparts.

Male-biased dimorphism was also present in aspects of prothoracic leg morphology (PFL, PTiL, PTiW, PTaL, PTaW). Enlarged protarsi covered in

adhesive setae are present in males of several groups of beetles (Stork 1980). The conspicuous male-biased dimorphism in tarsal size in *D. nigrrior* may result from sexual selection favoring larger tarsi due to increased ability to grasp the female during pre-copulatory resistance (Aiken and Khan 1992; Bergsten *et al.* 2001; Schulte-Hostedde and Alarie 2006). Similarly, longer profemora and protibiae may confer an advantage in grasping the female resulting in the dimorphism in these traits.

Male and female *D. nigrrior* differ in body shape. Although females have longer bodies and are heavier than males they are not simply larger versions of the male body morphology. This suggests different aspects of body size, rather than overall body size, are the targets of selection. A more elongated and deeper body design appears to be favored in females. Since body width is not sexually dimorphic, selection does not appear to favor larger overall body size in females but only longer and deeper bodies.

We are hesitant to make adaptive hypotheses about the relatively long pronota and trend towards relatively wider bodies in males as it seems likely that this shape dimorphism is caused by selection for a longer elytra length in females and not by selection for relatively longer pronota and wider bodies in males. Since females have elongated elytra (the largest component of SBL), the length of the pronotum would be longer for a given SBL in males (Kratochvil *et al.* 2003). Similarly, the trend towards relatively wider bodies in males may be the result of selection for longer, but not wider, bodies in females and not by selection for a relatively wide male body.

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