Sexual Size Dimorphism in the Diving Beetle *Laccophilus maculosus* Say (Coleoptera: Dytiscidae)

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Abstract

Sexual size dimorphism was quantified for a population of the diving beetle *Laccophilus maculosus* Say in Northern Ontario, Canada. Consistent with other populations of this species, but in contrast to the general pattern in insects, males were significantly larger than females in terms of body length, elytral length, and pronotal width. There was a significant multivariate difference in body size between the sexes, and discriminant function analysis identified 68.87% of individuals as the correct sex based on measurements of body size. Males also had significantly longer femora, longer tibiae, and larger tarsi on the pro- and mesothoracic legs.

Sexual selection arises from variance in reproductive success and is a potent force in the evolution of morphology in sexually reproducing species (Andersson 1994). Sexual selection is typically greater in males than females and its effects on morphology are typically most evident in males (Andersson 1994). Much of the difference in morphology between the sexes, including larger and more elaborate traits in males, and larger body size in males is commonly attributed to sexual selection (Andersson 1994).

Sexual size dimorphism (SSD) in body size is widespread in the animal kingdom with variation in degree and direction among species (Hedrick and Temeles 1989; Andersson 1994; Fairbairn 1997; Teder and Tammaru 2005) and even among populations of a single species (Fairbairn and Preziosi 1994; Pearson *et al.*, 2002; Krause *et al.* 2003; Fairbairn 2005). There is a general pattern of male-biased SSD in homoiotherms (Price 1984; Shine 1994). This pattern is often attributed to sexual selection for larger body size in males (Andersson 1994). Female-biased SSD dominates in poikilotherms (Wiklund and Karlsson 1988; Fairbairn 1990). For example, a survey of SSD in insects showed that 81.6% of 158 species included had consistent female-biased SSD, while only 7.6% had consistent male-biased SSD (Teder and Tammaru 2005). This pattern is often thought to be the result of fecundity selection favoring larger body size in females (Honek 1993; Andersson 1994; Blanckenhorn 2000). However, sexual selection for larger body size in males can be present in species with female-biased SSD (Karban 1983; Howard and Kluge 1985), and fecundity selection for larger body size in females can be present in species with male-biased SSD (Harvey 1990) suggesting that the sexual selection and fecundity selection alone are not sufficient to explain patterns of SSD. It is likely that there is selection for larger body size in both and males and females of many species, with the evolution of larger body size being constrained by selection against larger body size (Blanckenhorn 2000). Sexual size dimorphism should exist when natural and sexual selection for and

against larger body size reach different equilibria in males and females (Price 1984; Arak 1988; Schluter *et al.* 1991; Blanckenhorn 2000; Blanckenhorn 2005). Similarly, there is likely selection for and against larger size in particular morphological traits with sex size differences resulting when the selection pressures reach different equilibrium in males and females.

The selective forces that cause the variation in direction and degree of SSD among animal species are not fully understood. Species that exhibit SSD counter to general patterns, and taxa containing both species with male-biased SSD and female-biased SSD, may be particularly valuable to a better understanding of the evolution and maintenance of SSD.

Predaceous diving beetles (Dytiscidae) are one of the largest and most commonly encountered groups of aquatic beetles. Difference in body size between the sexes is often not conspicuous but there are examples of both female-biased (Schulte-Hostedde and Alarie 2006) and male-biased (Zimmerman 1970; Aiken and Wilkinson 1985; Juliano 1992) SSD. Descriptions and statistical tests of sex differences in body size are missing for many dytiscid species.

There is often conspicuous dimorphism in the pro- and sometimes mesotarsi in dytiscids with males possessing enlarged tarsi equipped with modified adhesive setae used to grasp the dorsal surface of females during mating behavior (Stork 1980; Aiken 1992; Larson *et al.* 2000; Bergsten *et al.* 2001; Miller 2003). A larger surface area for attachment of adhesive setae may allow for a greater number, or greater size, of adhesive setae which may result in greater adhesion to the dorsal surface of the female. Thus, larger protarsi may be favored by sexual selection. There is some evidence that larger tarsi may be favored by sexual selection in dytiscids (Schulte-Hostedde and Alarie 2006), however experimental support of this hypothesis is not available. A study using a mating experiment and allometry yielded no evidence that larger tarsi were favored in a whirligig beetle (Coleoptera: Gyrinidae) (Fairn *et al.* 2007a). There is a wide range in degree of enlargement of pro- and mesotarsi in male dytiscids (Larson *et al.* 2000) but the actual degree of sexual size dimorphism is not known for many species. Differences in degree of dimorphism between species may have important implications for studies of phylogeny, sexual selection, sexual conflict.

Males in water beetles species where males have enlarged tarsi used to grasp females may also have larger femora and tibiae on legs that bear the enlarged tarsi. For example, males of the dytiscid species *Dytiscus alaskanus* possess relatively longer profemora than females (Aiken and Wilkinson 1985), and males of the whirligig beetle *Dineutus nigrior* (Coleoptera: Gyrinidae) have longer femora, and longer and wider tibiae on legs that bear enlarged tarsi despite being smaller than females in overall body size (Fairn *et al.* 2007b).

The dytiscid species *Laccophilus maculosus* Say is a small dytiscid with prominent pale areas along lateral, basal, and sutural margins of the elytra (see Figure 7 in Larson *et al.* 2000 for dorsal habitus). This species prefers warm, shallow, vegetated areas of permanent, lentic systems (Larson *et al.* 2000) and is present throughout much of North America (Zimmerman 1970). Mean measurements of body length, elytral length, body width, and pronotal width for males and females from throughout North America have been reported and male means were generally larger for all measured traits (Zimmerman 1970). However, to our knowledge evidence of statistical significance of the larger size in males is not available in the literature and measurements from several areas of the geographic range, including Northern Ontario, are not available. Male pro- and mesotarsi in *L. maculosus* are conspicuously enlarged in a dorsoventral plane and

are equipped with adhesive setae on the ventral surface used to hold the female during mating behavior (Zimmerman 1970). To our knowledge the degree of sexual size dimorphism in the pro- and mesotarsi has not been quantified for this species and sexual dimorphism in tibiae and femora has not been described.

Here we investigate sexual size dimorphism in terms of body size and leg components in a population of *L. maculosus* from Northern Ontario, Canada. The main objectives of this study were (1) to use univariate and multivariate methods to test for the significance of larger male body size in this species and (2) to quantify the degree of dimorphism in the pro- and mesotarsi and to test the hypothesis that femora and tibiae of legs that posses enlarged tarsi are also enlarged.

Methods

Measurements. We collected adult *L. maculosus* in late June, 2006 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. Beetles were collected by sweeping areas of submergent and emergent vegetation with nets. We transported the specimens alive to the lab and all specimens were euthanized in the lab with 70% ethanol. Tibia and tarsomere measurements were obtained using a micrometer equipped compound microscope (Olympus BX50). All other measurements were obtained using a micrometer-equipped research stereo microscope (Wild M3C). 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. All leg measurements were performed on the right leg. Tarsomere measurements were made on the second tarsomere. The characters and terms used are as follows:

Body size measurements
   Head length (HL): measured dorsally along mid-line, not including mouthparts
   Head width (HW): measured at greatest transverse width
   Pronotal length (PL): measured dorsally along mid-line
   Pronotal width (PW): measured at greatest transverse width
   Elytral length (EL): measured dorsally along mid-line
   Elytral width (EW): maximum transverse width measured dorsally across both elytra
   Standardized Body length (SBL): sum of HL + PL + EL

Leg measurements
   Profemur length (PFL): measured along anterior margin
   Mesofemur length (MsFL): measured along anterior margin
   Metafemur length (MtFL): measured along anterior margin
   Protibia length (PTiL): measured along anterior margin
   Mesotibia length (MsTiL): measured along anterior margin
   Protarsomere length (PTL): greatest linear distance measured along mid-line
   Protarsomere height (PTH): greatest distance between ventral and dorsal surface
   Mesotarsomere length (MsTL): greatest linear distance measured along mid-line
   Mesotarsomere height (MsTH): greatest distance between ventral and dorsal surface
   Statistical analysis. All variables were $\log_{10}$-transformed to improve normality. We tested for dimorphism in trait size using independent *t*-tests. Discriminant function analysis (DFA) was performed to determine if the six body size variables

(HL, HW, PL, PW, EL, EW) 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).

Results

The mean size of all traits measured was larger in males than females. Elytral length, PW, SBL, and all measured components of the pro- and mesothoracic legs were statistically larger (Table 1). Trait means ranged from 0.1–39.6% larger in males than females, with pro- and mesothoracic leg components exhibiting the highest degree of dimorphism (Figure 1).

While the means were larger in males, the range was generally fairly similar between the sexes with a large amount of overlap for body size traits. There was less overlap for components of the pro- and mesothoracic legs, and for PTiL, PTH, and MsTH there was no overlap between the sexes (Table 1). The mean measurements in this population were generally fairly similar to measurements from other populations (Zimmerman 1970).

There was a significant multivariate difference between the sexes in terms of body size (Wilks lambda = 0.842, $F_{(6,99)}$ = 3.10, P = 0.008). The squared Mahalanobis distance between male and female centroids was 8.12. The DFA was able to identify 68.87% of the specimens as the correct sex (68.12% of females, 70.27% of males). All variables were negatively correlated with the canonical vector (Table 2). The mean canonical score for males was −0.587, and 0.315 for females. The distribution of canonical scores is presented in Figure 2.

Discussion

Body size measurements

We demonstrate that males have larger mean size in a variety of body size traits in this population in Northern Ontario providing support for the hypothesis that there is male-biased SSD throughout the range of this species. We also provide data suggesting that the male-biased SSD is statistically significant for several components of body size. Our results, combined with previous studies, suggest that the male-biased SSD may be a significant and consistent pattern in this species. Therefore, sources of selection on body size appear to reach different equilibria in the two sexes. Male-biased SSD is commonly attributed to strong sexual selection for larger body size in males (Andersson 1994). If selection against large body size is equal for males and females then male-biased SSD could result from sexual selection for larger body size in males being greater than fecundity selection for larger body size in females (Blanckenhorn 2005). However, we are not aware of studies documenting the mating behavior or sexual selection pressures in this species, or of studies addressing the relationship between body size and fecundity, and thus speculation on the importance of these sources of selection on the pattern of SSD would be difficult. It is also possible that sources of selection against larger body size are stronger in females than males. However, due to the paucity of studies of the ecology of this species we do not know if this is likely.

Another possible cause of the male-biased SSD is that there is natural selection favoring divergence in body size between the sexes. One possibility is that

Table 1. Means (± 2 SE) (back transformed from $\log_{10}$-transformed data) and ranges for morphological traits of male and female *Laccophilus maculosus*. Units for all traits are mm. The results of independent *t*-tests for differences between the sexes are also provided.

Trait	Female				Male				*t*-value
	n	Mean	± 2 SE	Range	n	Mean	± 2 SE	Range	
EL	107	4.11	4.08–4.13	3.81–4.37	67	4.15	4.12–4.17	3.89–4.40	2.76**
EW	104	3.08	3.06–3.10	2.89–3.26	59	3.09	3.07–3.11	2.92–3.33	0.628
PL	77	0.983	0.975–0.992	0.833–1.05	47	0.995	0.984–1.01	0.881–1.07	1.65
PW	73	2.41	2.40–2.43	2.19–2.59	46	2.44	2.42–2.46	2.19–2.59	2.2*
HL	72	0.902	0.894–0.91	0.809–0.952	46	0.906	0.896–0.916	0.857–0.976	0.588
HW	72	1.63	1.63–1.64	1.55–1.74	47	1.64	1.63–1.65	1.55–1.74	0.882
SBL	70	6.00	5.97–6.03	5.67–6.34	45	6.07	6.03–6.12	5.69–6.45	2.55*
PFL	23	0.892	0.875–0.909	0.809–0.952	24	0.944	0.930–0.957	0.881–1.05	4.73***
MsFL	25	1.00	0.988–1.02	0.928–1.07	23	1.03	1.02–1.05	0.952–1.09	2.81**
MtFL	47	0.802	0.793–0.810	0.738–0.857	39	0.803	0.792–0.814	0.738–0.904	0.19
PTiL	20	0.677	0.669–0.685	0.644–0.713	12	0.703	0.690–0.716	0.673–0.733	3.5**
MsTiL	19	0.685	0.676–0.695	0.653–0.743	8	0.721	0.706–0.737	0.693–0.752	4.03***
PTL	25	0.117	0.114–0.121	0.104–0.134	12	0.144	0.139–0.149	0.134–0.158	8.49***
PTH	25	0.091	0.088–0.093	0.079–0.099	12	0.127	0.124–0.130	0.119–0.134	15.22***
MsTL	23	0.139	0.136–0.141	0.129–0.154	10	0.151	0.145–0.157	0.144–0.173	4.63***
MsTH	23	0.099	0.096–0.102	0.079–0.109	10	0.133	0.128–0.138	0.119–0.149	11.65***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
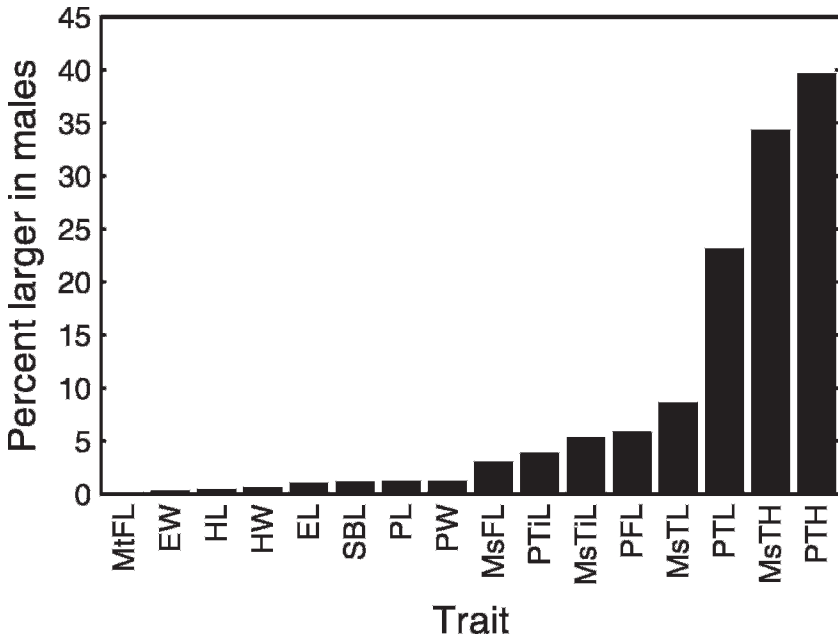
Fig. 1. Degree of dimorphism for all body and leg traits. Trait means ranged from 0.1–39.6% larger in males than females. Results for tests of significance of difference in trait size are found in Table 1.

copulating or guarding pairs may have better swimming speed and maneuverability when the male is larger than the female and therefore larger males and smaller females are favored by natural selection (Adams and Greenwood 1983). Ecological niche divergence between the sexes to decrease competition for resources could also result in sexual size dimorphism if the optimal body size differs for the different niches (Slatkin 1984; Shine 1989).

To fully understand the selective pressures resulting in the male-biased SSD in this species a study of lifetime selection on body size in males and females (cf. Preziosi and Fairbairn 2000) is required. We suggest that dytiscids may be an excellent group for the study of the evolution and maintenance of SSD as there are examples of both male-biased and female-biased SSD. However, more work is needed to quantify SSD in dytiscid species to elucidate broad patterns of SSD in

Table 2. Factor structure of canonical vector for six body size components.

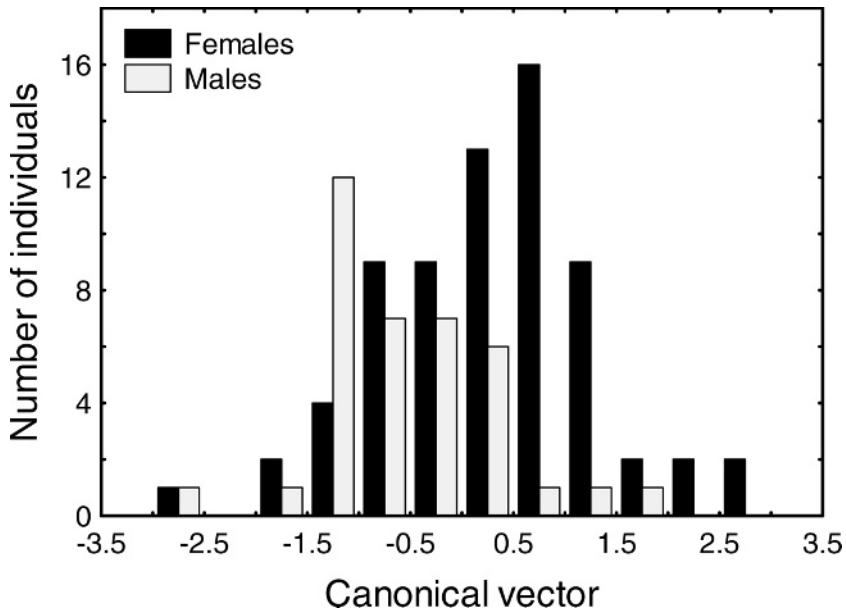| Trait	Canonical structure
EL	−0.576
EW	−0.119
PL	−0.452
PW	−0.640
HL	−0.089
HW	−0.229

Fig. 2. Frequency distribution of canonical discriminant scores for male and female *Laccophilus maculosus*. Female mean = 0.315, male mean = −0.587.

the group. Also, studies on the life history of dytiscid species, particularly mating and reproductive aspects, are essential.

Leg measurements

Male *L. maculosus* were significantly larger than females in terms of pro- and mesothoracic leg components. The degree of dimorphism in these traits was greater than for body traits which suggests that these traits are not larger simply because body size is larger. This suggests that selection for larger size in these traits is stronger in males than females in relation to the selection against larger size.

While it is possible that non-sexual selection pressures on pro- and mesothoracic leg size are different on males and females (*e.g.* ecological niche divergence) we believe that sexual selection for larger size in male traits is the more likely explanation for the male-biased size dimorphism. When a morphological trait is larger in males than the homologous trait in females it is often thought to be caused by sexual selection favoring larger trait size in males (Andersson 1994). This is especially likely when the trait has obvious use in activities that are related to mating success. Since pro- and mesothoracic legs are used to grasp the female during mating it seems likely that sexual selection may be important in the evolution of larger size in these traits in males.

Adhesive setae are located on the ventral surface of pro- and mesotarsomeres in four rows with what appeared to be four setae per row. Tarsomere 1 bears two rows of setae, and tarsomeres 2 and 3 bear one row each. The area available for attachment of setae can be described by the length × width of the ventral surface of the first three tarsomeres. We were able to measure tarsomere length but

unfortunately we were not able to measure the width of the ventral surface due to the very small size and difficulty in orienting the trait in such a way that measurements could be accurately taken. Tarsomere length was significantly larger in males. Longer tarsomeres did not seem to allow for a greater number of adhesive setae as the number of rows was consistent in all specimens. However, longer tarsomeres may allow for larger size of adhesive setae. The height of the tarsomere was also larger in males. While greater height does not increase the surface area available for adhesive setae, it may allow for greater musculature which could result in greater strength to grasp the female. It is possible that selection favors larger size in only one dimension of tarsomere size and that other dimensions are larger due to a genetic correlation with the dimension that is directly selected for.

Males also had longer femora and tibiae on the pro- and mesothoracic legs but metafemora were not longer in males. The metathoracic legs are used for swimming and do not bear modified adhesive setae, and are not used to grasp the female. This suggests that the strong dimorphism in the femora and tibiae of the pro- and mesothoracic legs is related to the function of grasping the female, and is not a pattern of leg components in general.

There are several potential hypotheses for the cause of enlarged femora and tibiae on legs that bear enlarged tarsi. First, longer femora and tibiae may be advantageous in increasing the reach of the legs to grasp females at a greater distance, or to better reach around the body of the female during mating behavior. For example, the *D. alaskanus* males have relatively long profemora presumably to allow males to grip the edge of the female pronotum in the femur-tibia joint during mating behavior (Aiken and Wilkinson 1985). Second, longer femora and tibiae may allow for greater leg musculature and hence greater strength to grasp and hold the female, or to support the enlarged tarsi. Third, there may be a genetic correlation between the size of the tarsomeres and other leg characteristics and if selection favors larger tarsomeres, larger tibiae and femora may result even if those traits do not confer an advantage.

If there is contemporary sexual selection favoring larger size in pro- and mesothoracic leg components, males with larger traits should have increased mating success. This could be tested through experimental studies, or through comparison of trait size of males collected in copula in the field to males not in copula. Since it is likely that size of some leg components are correlated it is crucial to control for the size of other leg traits when determining if a particular trait is directly selected. This could be done through the use of multivariate selection coefficients (Lande and Arnold 1983; Preziosi and Fairbairn 2000).

Acknowledgements

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