Quantitative Analysis of Sexual Dimorphism and Sex Ratio in Hyphydrus ovatus (Coleoptera: Dytiscidae)

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Sexual dimorphism in size, shape, and mass relative to length, and sex ratios are quantified for populations of *Hyphydrus ovatus*, a dytiscid beetle. Males of *H. ovatus* are not only longer than females, but also significantly larger in elytron length, thorax width, head width, leg length, total width, total depth, and abdominal segment length. Two local populations differ slightly but significantly in total depth and abdominal segment length, but sexual dimorphism in size is similar for the two populations. *Hyphydrus ovatus* are also sexually dimorphic in shape, with males having relatively broader heads and thoraxes than females. The two populations differed slightly but significantly in relative abdominal segment length, but as with size, sexual dimorphism in shape is similar for the two populations. Males are relatively heavier than females, although the slope of the log mass vs log length relationship is the same for the two sexes. Sex ratios in field samples vary significantly over the summer, with percent females declining from c. 50% to c. 15%. Sex ratios are significantly below 50% females in two of five monthly samples and in the total pooled set of samples. Sexual dimorphism in size, shape, and relative mass, combined with male-biased sex ratios suggest that larger size of male *H. ovatus* is a product of sexual selection.

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Introduction

Darwin (1874) noted that sexual size dimorphism in invertebrates overwhelmingly involves larger females. There are, however, arthropod species in which males are the larger sex (e.g. Darwin 1874, Arrow 1951, Otte and Stayman 1979, Johnson 1982, Adams and Greenwood 1983, Forrest 1987, Zeh 1987, Wiklund and Forsberg 1991). It is typically assumed that when males are the larger sex, this condition is a result of some form of sexual selection, usually involving male-male competition (Adams and Greenwood 1983). Although sexual selection is the most commonly proposed cause of sexual size dimorphism, other causes, such as intersexual resource partitioning (Shine 1989), intersexual differences in growth rates (Kozlowski 1989), or mechanical constraints resulting from which sex carries the other

during copulation (Adams and Greenwood 1983, Wiklund and Forsberg 1991) are possible. Body size is related to many aspects of an organism's life (Peters 1983), and interpreting differences in such general characters may be difficult.

Among arthropods in which males are larger, sexual dimorphism in size is often accompanied by obvious dimorphism in shape, with males having enlarged structures for male-male combat. Horns and enlarged mandibles in male scarabaeid and lucanid beetles (Arrow 1951, Eberhard 1979, Otte and Stayman 1979, Cook 1987), enlarged pedipalps in male pseudoscorpions (Zeh 1987), and intersexual differences in snout length and width in brentid weevils (Johnson 1982) are all related to male combat. Morphometric analysis of dimorphism in shape, as well as in size, is necessary in order to understand how the sexes differ.

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Sexual dimorphism in size is often based on measurement of one linear dimension, such as total length. However, in some species, males are larger in linear dimensions, but smaller in mass relative to length (Johnson 1982, Forrest 1987). Because the relationship between length and mass has been analyzed in relatively few sexually dimorphic species, the generality of this pattern is unknown.

The intensity of sexual selection by male-male competition is correlated with population sex ratio (Emlen and Oring 1977, Crespi 1989). Male-biased sex ratios may provide additional evidence for sexual selection as the cause of size dimorphism (Crespi 1989).

The dytiscid genus *Hyphydrus* consists of 97 species (Bistrom 1982a). Nearly all are sexually dimorphic for surface microsculpture (Bistrom 1982a,b). Many *Hyphydrus* spp. are also sexually dimorphic in body length, with males larger than females (Bistrom 1982a). There is no documented structural or behavioral evidence for sexual selection in this genus. There has been no quantitative analysis of sexual dimorphism in size or shape for any *Hyphydrus* species, and there has been no investigation of the mechanism producing this unusual (for insects) pattern of sexual size dimorphism. In this paper, I will address the first point by conducting a quantitative analysis of sexual dimorphism in *Hyphydrus ovatus* (Linnaeus), a common European species. I will address the following questions: 1) are *H. ovatus* also sexually dimorphic in shape, and if so, in which dimensions? 2) Are *H. ovatus* also sexually dimorphic in body mass, corrected for differences in length? 3) What is the typical sex ratio in natural populations of *H. ovatus* and does the sex ratio suggest that sexual selection causes sexual dimorphism in this species?

Study organism and methods

Hyphydrus ovatus is found throughout the Palearctic realm in large lentic bodies of water (Bistrom 1982a). Adults are 3.9 to 5.3 mm long, and are globular in shape (Bistrom 1982a). Mating occurs in spring and summer and larvae appear in summer (Juliano and Lawton 1990). Both adults and larvae prey upon small invertebrates (Bistrom 1982a, Juliano and Lawton 1990). Adults can fly and appear to live for 1½ yr (Bistrom 1982a).

The main study site was Pocklington Canal, near Bielby, Humberside, England. This slowly flowing navigation channel is connected to the River Derwent. At Bielby the canal is c. 10 m wide, with steep sides and is unshaded. Vegetation was described by Juliano and Lawton (1990). A secondary study site was a gravel pit also located in Humberside, c. 4 km from Pocklington Canal. This site has no detectable water flow, a gravel bottom, sparse marginal vegetation including grasses and sedges.

In order to verify that the Pocklington Canal population of *H. ovatus*, like others, is dimorphic in total body length, lengths of individuals collected at Pocklington Canal on 8 April 1988 (and subsequently used in the field experiment described by Juliano and Lawton (1990)) were determined.

Sexual dimorphism in multivariate size and shape was analyzed using multivariate analysis of variance (MANOVA) on size and shape variables. Size variables were measured for a sample of 30 ♀♀ and 58 ♂♂ collected at Pocklington Canal and Gravel Pit in summer 1988. The size variables were: elytron length, maximum width, head width, maximum dorso-ventral depth, length of abdominal sternite 1, and hind femur length. All measurements were made with an eyepiece micrometer on a dissecting microscope, and were log transformed for analysis. Shape variables were derived from size variables by taking the difference between logs of each size variable and log elytron (Mosimann and James 1979). This results in variables representing the logs of size variables expressed as proportions of elytron length (Mosimann and James 1979). Differences in such variables therefore indicate shape differences. Two way univariate ANOVA's and MANOVA were used to test for differences between the sexes, between sites, and for interaction.

Sexual dimorphism in mass relative to length was analyzed on a sample of 11 ♀♀ and 13 ♂♂ collected at Pocklington Canal on 6 and 7 May 1988. Lengths were measured as before, and fresh masses determined to the nearest 0.0005 mg. Masses and lengths were log transformed and analysis of covariance was used to test for a difference between the sexes in mass relative to length.

Sex ratios were compared for samples taken in autumn 1987 and spring and summer 1988 at Pocklington Canal. First, a G-test for heterogeneity of sex ratios across dates was used to test for changes in sex ratio over time. Second, G-tests of the null hypothesis of a 1:1 sex ratio were performed on samples from each date, and on the entire pooled sample. Third, a single sample of *H. ovatus* collected at the Gravel Pit site was tested for a 1:1 sex ratio, and then compared using a G-test for heterogeneity between sites with a sample from Pocklington Canal on the same date.

Results

Hyphydrus ovatus in the Pocklington Canal population were clearly dimorphic in total body length, as expected. Males measured (mean ± SE) 4.70 ± 0.01 mm (n = 77) whereas females measured 4.33 ± 0.01 mm (n = 75), and this difference was statistically significant (t = 19.51, df = 150, p < 0.0001).

In addition to dimorphism in body length, *H. ovatus* in these populations were dimorphic in multivariate size (Wilk's Lambda = 0.1309, p = 0.0001). All seven size

Table 1. Least squares means (± 2 SE) for size variables for sexes and populations, back transformed. ± 2 SE intervals are asymmetrical around the mean because of back transformation from logarithms to the natural (mm) scale. Significant differences (F-tests) between sexes or populations are indicated by: * = p<0.05; ** = p<0.01; *** = p<0.001; **** = p<0.0001.

	Thorax width	Head width	Maximum width	Abdomen lenght	Leg length	Maximum depth	Elytron length
♀♀							
	2.00	1.33	2.81	0.91	1.26	2.14	2.95
	(1.98,2.02)	(1.31,1.34)	(2.78,2.83)	(0.90,0.92)	(1.25,1.27)	(2.12,2.16)	(2.91,2.99)
	****	****	****	****	****	****	****
♂♂							
	2.24	1.44	3.04	0.98	1.36	2.31	3.15
	(2.22,2.25)	(1.43,1.45)	(3.02,3.07)	(0.97,0.99)	(1.35,1.37)	(2.29,2.33)	(3.12,3.18)
Gravel Pit							
	2.11	1.38	2.92	0.96	1.31	2.21	3.04
	(2.09,2.13)	(1.37,1.39)	(2.89,2.95)	(0.95,0.97)	(1.30,1.32)	(2.19,2.23)	(3.00,3.08)
				****		**	
Pocklington Canal							
	2.11	1.39	2.93	0.93	1.30	2.24	3.06
	(2.10,2.13)	(1.38,1.40)	(2.91,2.95)	(0.92,0.94)	(1.30,1.31)	(2.23,2.26)	(3.03,3.10)

variables yielded significant sex effects (Table 1) and males were larger than females in all dimensions (Table 1). In addition, there was a significant multivariate population effect (Wilk's Lambda = 0.6387, p = 0.0001). Abdomen length and dorso-ventral depth differed significantly between populations in univariate analyses (Table 1), with the Gravel Pit population having a larger abdominal segment length, and the Pocklington Canal population having a greater body depth (Table 1). Interactions of sex and population were not significant (Wilk's Lambda = 0.9107, p = 0.3861). Thus, the sexes differ in all aspects of size, and the two populations differ in two of seven measures of size, and the differences between the sexes is independent of population.

Multivariate shape analysis indicated a significant difference between the sexes (Wilk's Lambda = 0.4316, p = 0.0001). In univariate analyses, two shape variables – relative thorax width and relative head width – differed significantly between the sexes (Table 2), with males having greater relative widths than females (Table 2). Multivariate shape analyses also showed a significant difference between populations (Wilk's Lambda = 0.6502, p = 0.0001). Only one shape variable – relative abdominal segment length – differed significantly between populations in univariate analyses (Table 2), with the Gravel Pit population having relatively larger abdominal segments (Table 2). Interactions of sex and population were not significant (Wilk's Lambda = 0.9183, p = 0.3297). Thus, the sexes differ in two of six measures of shape, populations differ in one

Table 2. Least squares means (± 2 SE) for shape variables for sexes and populations, back transformed. ± 2 SE intervals are asymmetrical around the mean because of back transformation from logarithms to the natural (proportion) scale. Significant differences between sexes or populations are indicated as in Table 1.

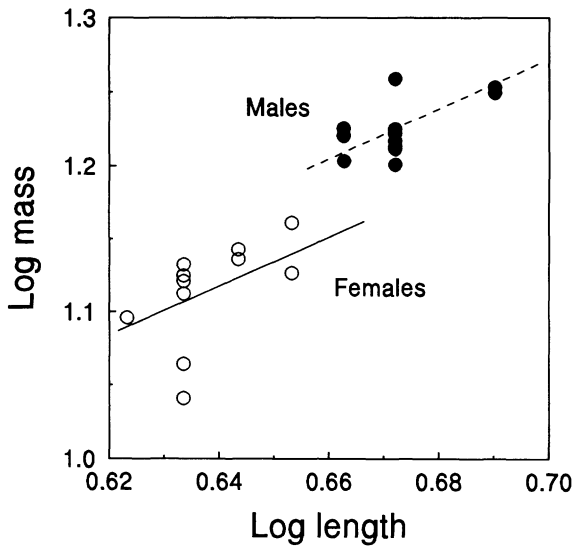|	Relative thorax width	Relative head width	Relative maximum width	Relative abdomen length	Relative leg length	Relative maximum depth
♀♀						
	0.68	0.45	0.95	0.31	0.43	0.73
	(0.67,0.69)	(0.44,0.45)	(0.94,0.96)	(0.30,0.31)	(0.42,0.43)	(0.72,0.74)
	****	*				
♂♂						
	0.71	0.46	0.97	0.31	0.43	0.73
	(0.70,0.72)	(0.45,0.46)	(0.96,0.98)	(0.31,0.31)	(0.43,0.44)	(0.72,0.74)
Gravel Pit						
	0.70	0.45	0.96	0.31	0.43	0.73
	(0.69,0.71)	(0.45,0.46)	(0.95,0.97)	(0.31,0.32)	(0.43,0.44)	(0.72,0.74)
				***		
Pocklington Canal						
	0.69	0.45	0.96	0.30	0.43	0.73
	(0.68,0.70)	(0.45,0.46)	(0.95,0.97)	(0.30,0.31)	(0.42,0.43)	(0.72,0.74)

Fig. 1. Relationship between mass and total length for males and females of *Hyphydrus ovatus*. Values are log transformed (base 10). Fitted lines are the result of analysis of covariance.

measure of shape, and the differences between the sexes is independent of population.

H. ovatus was also sexually dimorphic for mass corrected for length. Because slopes of the log mass vs log length relationship did not differ between the sexes ($F_{1,20} = 0.70$, $p = 0.4130$), analysis of covariance was appropriate. Analysis of covariance indicated that log mass increased significantly with log length ($F_{1,21} = 9.54$, $p = 0.0001$, slope $= 1.66 \pm 0.54$), and that there was a significant difference between the sexes in the elevations of the parallel regression lines ($F_{1,21} = 6.88$, $p = 0.0159$). Males were clearly heavier for their length than were females (Fig. 1). Back transformed least squares means (SAS Institute Inc. 1987) were ($\pm$ SE, back transformed): $\male\male$ 15.81 mg (15.43 mg, 16.20 mg); $\female\female$13.96 mg (13.58 mg, 14.36 mg). These means correspond to expected masses of males and females at the overall mean length for the population (4.53 mm). Thus, at this length, males average 1.85 mg (13.2%) heavier than females.

Sex ratios at Pocklington Canal varied significantly across dates (G for heterogeneity = 11.86, df = 4, $p = 0.0185$). Sex ratios on individual dates (Fig. 2) appeared to decline from spring values near 50% $\female\female$, to late summer and autumn values of 12 to 16% $\female\female$. G-tests on individual dates indicated that the samples taken in September 1987 (G = 9.817, df = 1, p < 0.005) and June 1988 (G = 6.111, df = 1, p < 0.025) differed significantly from a 1:1 sex ratio, but that samples from all other dates did not differ significantly from a 1:1 sex ratio (p > 0.05) (Fig. 2). Across all dates pooled, the sex ratio departed significantly from 1:1 (G = 9.140, df = 1, $p = 0.0025$), and 43.7% of all individuals collected were $\female\female$. One sample collected from the Gravel Pit pop-

ulation on 10 June 1988 was composed of $39.3 \pm 9.2\%$ $\female\female$, and thus had a similar sex ratio to the sample collected from the Pocklington Canal population on the same date (compare to Fig. 2). The Gravel Pit sample did not depart significantly from a 1:1 sex ratio (G = 1.273, df = 1, p > 0.05), probably because of the smaller sample size. Sex ratios in these two samples did not differ significantly (G = 0.085, df = 1, p >> 0.05), suggesting that sex ratios in separate populations are similar at the same time of year.

Discussion

In addition to the well known sexual dimorphism in total length, *H. ovatus* males are larger in all dimensions, have relatively broader heads and thoraxes, and are relatively heavier than females. Although there have been few quantitative studies of sexually dimorphic insects, the sexual dimorphism observed in *H. ovatus* appears unusual compared to other insects in which males are larger.

The intersexual differences in shape in *H. ovatus* are subtle and do not strongly suggest male-male combat. Other causes for sexual dimorphism in shape seem possible. For example, the relatively and absolutely broader head and thorax of the male may enable males to feed on larger prey than do females. Although such intersexual resource partitioning has been proposed as an explanation of sexual dimorphism in many groups (Shine 1989) it has not, to my knowledge, been proposed for any insect in which males are the larger sex.
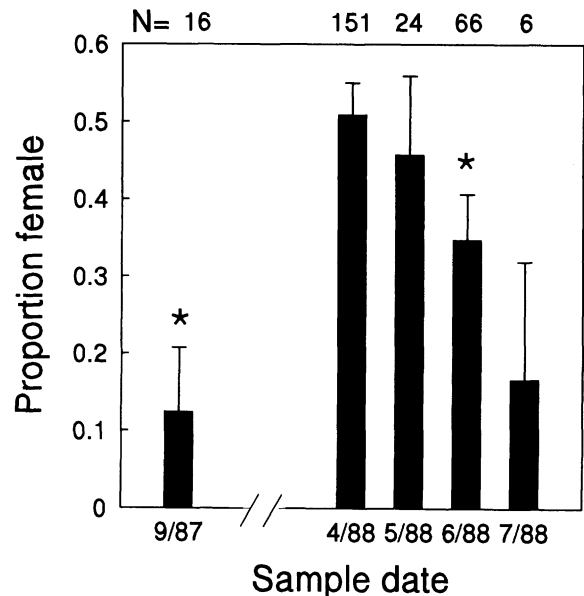

Fig. 2. Percent females ($\pm$ SE) in samples of *Hyphydrus ovatus* from Pocklington Canal. * – sample percent significantly different from 50% (G-test).

The hypothesis of intersexual resource partitioning requires that resource competition occurs. However, food limitation and competition seem unlikely to occur at natural densities of *H. ovatus* at Pocklington Canal (Juliano and Lawton 1990). An alternative hypothesis is that males are larger than females because copulating pairs with larger males have superior swimming performance (Adams and Greenwood 1983). Although there is at present, no evidence against this hypothesis, the observed dimorphism in shape is not a necessary prediction of this hypothesis.

Another unusual aspect of sexual dimorphism in *H. ovatus* is that males are relatively heavier than females. Even though males are the larger sex in total length in mole crickets (Forrest 1987) and brentid weevils (Johnson 1982), males are relatively lighter than females in these species. Male *H. ovatus* may be relatively heavier than females due to their relatively broader heads and thoraxes, or due to differences in body composition. Although males have a lower percentage of body fat than females (Juliano and Lawton 1990) it is not known what other body composition differences (e.g. greater percentage of exoskeleton or protein mass in males) are correlated with this difference.

Sex ratios of *H. ovatus* tend to be male biased, suggesting that intrasexual selection and male-male competition are likely (Crespi 1989). The sex ratio changes over time, with the proportion of females declining from spring to autumn, suggesting that if sexual selection occurs, it is more intense later in the year. Whether proportion of females declines due to selective mortality or due to dispersal by mated females to specific oviposition sites (e.g., Snead and Alcock 1985) is unknown.

Almost nothing is known about the courtship and mating behavior of *H. ovatus*, and it is possible that some form of male-male combat does occur. Even if direct male-male combat does not occur, the combination of larger male size, and male-biased sex ratios suggest that sexual selection acts on males. Males of many insects guard females immediately after mating (e.g. Johnson 1982, Crespi 1989), and larger males may have an advantage in such guarding. Male dytiscids mount females dorsally when mating, and larger, relatively broader males may be more successful at holding prospective mates. If larger males provide greater numbers of sperm, and females are polygamous, large males may have an advantage in sperm competition (Wiklund and Forsberg 1991). Female choice for larger males is also possible.

Clearly, sexual dimorphism in size in *H. ovatus* could be explained in several ways. The combination of larger, relatively heavier males, and male biased sex ratios indicates that some form of sexual selection is the most likely explanation, and behavioral studies of this species should focus on testing the hypothesis of sexual selection. Larger male size initially raises the question: why are males larger? However, this question could be

phrased in a completely different way: what constraints or costs favor smaller female size? In virtually all insects examined, larger females gain a fecundity advantage. Smaller female size in a species suggests that fitness of females increases with size more slowly than does fitness of males (Kozlowski 1989). The causes of this difference in size-dependent fitness may derive from females' ecology and behavior as well as from those of males.

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