Sexual dimorphism and allometry in the giant water strider *Gigantometra gigas*

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Abstract: This study describes sexual dimorphism in size (total body length and lengths of leg components) and in the allometric relationships between leg-component lengths and total body length in the giant water strider *Gigantometra gigas* (Heteroptera: Gerridae). *Gigantometra gigas* is the largest known gerrid, and has been previously described as monomorphic for body size. We compare our results with analogous data collected on *Gerris buenoi*, a species of more moderate size, where females are larger than males. Based on 94 specimens of *G. gigas*, we conclude that males are larger than females in all measured traits. This dimorphism was most spectacular in the leg components, which are 10–50% longer in males than in females. Males are generally more variable in size than females, and this is especially so for leg components. Allometric analysis suggests that total leg lengths (particularly middle and rear) increase at a much greater rate with body size in males than in females, therefore there is sexual dimorphism in allometries on the scale of that in the traits themselves. The relationship between middle and hind leg lengths is strong in both sexes, and appears to differ very little between the sexes or between *G. gigas*, and *Ge. buenoi*. These data suggest a constraint on this relationship, perhaps because of the biomechanics of locomotion. We propose that sexual selection acting on middle leg lengths in males explains both the increase and variance in middle leg length, and that hind leg length follows by correlated response.

Résumé : On trouvera ici la description du dimorphisme sexuel de la taille (taille du corps et taille des composantes des pattes) et des relations allométriques entre les composantes des pattes et la taille du corps chez le patineur *Gigantometra gigas* (Heteroptera : Gerridae). *Gigantometra gigas* est le patineur le plus grand que l'on connaisse et il a été décrit antérieurement comme monomorphe en fonction de sa taille. Nous comparons nos résultats à des données analogues obtenues chez une espèce de taille moyenne, *Gerris buenoi*, dont les femelles sont plus grosses que les mâles. D'après les mesures obtenues chez 94 *G. gigas*, les mâles sont plus grands que les femelles, et cela pour toutes les structures mesurées. Ce dimorphisme est particulièrement spectaculaire dans le cas des composantes des pattes, alors que les mâles ont des mesures de 10 à 50% plus grandes que celles des femelles. Les mâles sont généralement de taille plus variable que les femelles, particulièrement en ce qui concerne les mesures des pattes. L'analyse allométrique semble indiquer que la longueur des pattes (surtout la médiane et la postérieure) augmente en fonction de la taille du corps selon un taux beaucoup plus important chez les mâles que chez les femelles. Le dimorphisme sexuel dans l'allométrie suit donc la même échelle que celui que l'on observe dans les structures elles-mêmes. La relation entre la taille de la patte médiane et celle de la patte postérieure est donc forte chez les deux sexes et semble différer peu d'un sexe à l'autre ou d'une espèce à l'autre chez *G. gigas* et *Ge. buenoi*. Ces données indiquent l'existence d'une contrainte sur cette relation, peut-être reliée à la biomécanique de la locomotion. Nous croyons que la sélection sexuelle qui agit sur la longueur de la patte médiane du mâle peut expliquer à la fois l'augmentation de taille et l'augmentation de la variance de la longueur de la patte médiane et que la longueur de la patte postérieure varie de la même façon par corrélation.

[Traduit par la Rédaction]

Introduction

Sexual dimorphism is a conspicuous feature in the animal kingdom and is often attributed to sexual selection. Sexual selection drives morphological differentiation between the sexes if the dimorphic character functions mainly in one sex to confer a mating advantage on individuals with more extreme development of the character (e.g., Lande 1980; Andersson 1994). Evolution of the dimorphism is expected to occur until costs due to natural selection bring the process to a halt (reviewed in Andersson 1994). There are a number of examples of sexual dimorphism in insects, and sexual selection often underlies these dimorphisms (e.g. Fairbairn 1990; Sivinski and Dodson 1992; Zeh 1992; Nedved 1994; Emlen 1996).

In water striders (Gerridae), much research has focused on mechanisms leading to sexual dimorphism. Common throughout the Gerridae are sexual dimorphisms in various morphologies associated with grasping females during premating struggles (reviewed in Arnqvist 1997). Similarly, sexual selection on males for large body size has been demonstrated in several species (e.g. Fairbairn 1988; Arnqvist et al. 1996). Intriguingly, this is occurring in species in which females are

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larger than males, as is the norm for the Gerridae. Fairbairn (1997) has reviewed the hypotheses put forward to explain this pattern in gerrids and other taxa, and Andersen (1997) has tracked the evolution of size dimorphism in the phylogenies of the Gerridae.

Although females are typically larger than males within the Gerridae, there is a great deal of variation among species and apparent patterns in this variation. Within subfamiles of the Gerridae, the ratio of female size to male size appears to decrease as mean body size increases (Fairbairn 1990; Andersen 1997). This pattern is consistent with Rensch's (1960) rule, which predicts that sexual size dimorphism (SSD) will decrease with increasing body size in taxa in which females are the larger sex (hypoallometry) and increase with increasing body size in taxa in which males are the larger sex (hyperallometry). Because little research has been done on species of Gerridae in which males are the larger sex, it is currently not known whether or not this family also exhibits hyperallometry for SSD. In this study we present the first formal examination of sexual dimorphism and allometry in *Gigantometra gigas*, a water strider with male-biased SSD.

The largest water strider known, *G. gigas* is reported to be monomorphic for total body size (Andersen 1997). We know very little else about this giant water strider. A male *G. gigas* was first described in 1925 (China 1925) and was postulated to be the largest known water strider and the most basal of the subfamily Gerrinae. Based on the few male specimens available for study, it was found that *G. gigas* was the only member of the Gerrinae, and one of two members of the Gerridae, in which the hind legs were longer than the middle legs. A recent rediscovery of *G. gigas* in Vietnam has allowed a careful reexamination of male leg and body lengths, and the first characterization of these traits in females.

The purpose of this paper is to describe SSD for body and leg lengths and conduct an analysis of sexual dimorphism in allometric relationships of these traits. Allometric analysis can provide valuable information about patterns of character covariation (Klingenberg and Spence 1993). The relationship of a structure (Y) to another structure (X), taken as reference, is expressed by the formula $Y = \alpha X^{\beta}$, where α is a constant and β is the ratio of the two structures. From this formula is derived $\log Y = \log \alpha + \beta \log X$, and thus if there is a linear relationship between Y and X, we can make interspecific or intersexual comparisons based on the slope and intercept of the line. In our study, we are most interested in differences in slope between the sexes. As a reference point, we compare our data with those from a more characteristic species of water strider, *Gerris buenoi*, which is a member of the same subfamily, Gerrinae, as *G. gigas*, but females are larger than males.

Methods

Organisms

Gigantometra gigas lives on the surface of streams (Hoffmann 1936) and is endemic to regions of Vietnam and south China (Andersen 1982). Specimens were collected from streams in central Vietnam in October 1997. Males were both apterous and macropterous, but all collected females were macropterous. *Gerris buenoi*, the species chosen as a "typical" member of the subfamily Gerrinae, is partially bivoltine and common to both temporary and permanent habitats throughout much of North America (Spence 1989). *Gerris buenoi* is the one of the smallest of the Gerrinae, but of moderate size among the Gerridae. Specimens were collected from Holland Marsh in south-central Ontario in April 1998.

Data collection and analysis

Body length and lengths of the femur and tibia of the middle and hind legs of *G. gigas* were measured with vernier calipers. Body length was measured from the tip of the connexival spine to the articulation of the rostrum. Foreleg measurements in *G. gigas* and all measurements in *Ge. buenoi* were made with an ocular micrometer mounted in a dissecting microscope.

Statistical analyses were conducted using SYSTAT 6.0 (Wilkinson 1989). Distributions of the variables that we analyzed did not deviate significantly from normality. Variances between male and female *Ge. buenoi* were homoscedastic, but those between male and female *G. gigas* and also between winged and wingless male *G. gigas* were heteroscedastic.

We used Student's t test to compare the various traits between the sexes in *Ge. buenoi* and we tested for significant differences in traits in *G. gigas* using the Mann–Whitney test. In our analysis of allometry, we performed model II reduced major axis (RMA) regressions (Sokal and Rohlf 1981) of foreleg length on body length, middle leg length on body length, hind leg length on body length, and middle leg length on hind leg length for both species of water striders. Plots of the latter three analyses are included in the results. The standard errors of the slopes and intercepts are approximated from the model I regression analysis (Sokal and Rohlf 1981, p. 550). We used the Student's t test to test for significant differences amongst slopes between the sexes.

The sample sizes in the t and Mann–Whitney tests differ from those in the regression analyses because only whole specimens (those with no missing parts) were included in the regressions.

Results

Sexual dimorphism

Male *G. gigas* are significantly larger than females in total body length and all measured leg and leg-component lengths (Table 1). This difference is most pronounced in leg lengths. Male body length is 6.2% greater than females', but male leg components range from 14 to 48% longer than females' (Table 1). The difference in body size is largely the result of an increase in the range of male body sizes toward the larger end (Fig. 1). The smallest male is about the size of the smallest female, but the largest male is much larger than the largest female. Leg lengths are similarly highly variable in males relative to females; however, in contrast to body lengths, there is little overlap in leg lengths of males and females. The relatively large variation in male body and leg lengths is reflected in relatively high coefficients of variation (CV) for each trait (Table 1).

Incidentally, we found significant differences in all measured components between winged and wingless male *G. gigas*. Basic statistics and Mann–Whitney test results for the fore, middle, and hind leg and body length are listed in Table 2. Although wingless male *G. gigas* had significantly longer leg components and body than their winged counterparts (Table 2), removal of the data for wingless males from the regression did not significantly alter the results of the t tests showing significantly different slopes between the sexes. There-

Table 1. Sample sizes, means and standard deviations (SD), and coefficients of variation (CV) of leg-component lengths and body lengths for *Gigantometra gigas*, with the results of the Mann–Whitney test for significant differences between the sexes (*n* is the sample size).

	Males				Females					
Length	Mean (mm)	SD (mm)	CV (%)	*n*	Mean (mm)	SD (mm)	CV (%)	*n*	*p*	Dimorphism (% difference)
Forefemur	7.26	0.63	8.7	58	6.22	0.35	5.6	36	<0.001	14.3
Foretibia	6.16	0.52	8.4	58	5.11	0.26	5.1	36	<0.001	17.0
Total foreleg	15.20	1.32	8.7	57	12.77	0.64	5.0	36	<0.001	16.0
Middle femur	48.57	7.41	15.2	58	31.94	2.02	6.3	36	<0.001	34.2
Middle tibia	44.28	7.18	16.2	55	29.94	2.51	8.4	36	<0.001	32.4
Total middle leg	98.39	16.22	16.5	47	66.94	4.79	7.1	31	<001	32.0
Hind tibia	74.91	17.86	15.1	54	38.74	3.66	5.8	35	<001	48.3
Hind femur	48.51	7.31	23.8	58	31.51	1.82	9.5	35	<0.001	35.0
Total hind leg	126.40	25.87	20.5	42	72.84	5.32	7.3	25	<0.001	42.4
Body	34.08	2.55	7.5	58	31.97	1.52	5.0	36	<0.001	6.2

Table 2. Sample sizes, means and standard deviations (SD), and coefficients of variation (CV) of leg-component lengths and body length for winged and wingless male *Gigantometra gigas*.

	Winged males				Wingless males			
Length	Mean (mm)	SD (mm)	CV (%)	*n*	Mean (mm)	SD (mm)	CV (%)	*n*
Foreleg	14.71	1.41	9.6	32	15.84	0.89	5.61	25
Middle leg	85.10	10.07	11.8	25	113.45	3.68	3.25	22
Hind leg	108.98	22.52	20.66	23	147.47	6.92	4.69	19
Body	32.47	2.21	6.81	33	36.21	0.76	2.10	25

Note: All components are significantly different ($p < 0.001$, Mann–Whitney test).

fore, winged and wingless males were included in all allometric analyses.

Size dimorphisms in *Ge. buenoi* are opposite in direction to those in *G. gigas*: females are significantly larger than males in all measured components (Table 3). In contrast, however, here the greatest difference is in body length, and there is little variation in the degree of dimorphisms in lengths of leg components. Male body length is 16% less than that of females, and leg components of males are 4–7% smaller. In contrast to *G. gigas*, CVs for lengths do not differ greatly between the sexes or between body and leg lengths within species (Table 3). Finally, the increase in body length of females is not accompanied by a large increase in the range of lengths; in fact, there is little overlap in body length ranges between the sexes (Fig. 2).

Allometry

In male *G. gigas*, body length was a very good predictor of middle and hind leg lengths ($r^2 = 0.96$ and 0.97, respectively, $p < 0.05$). Although female body length was also a good predictor of female middle and hind leg lengths, the r^2 values of regressions for females (0.89 and 0.90, respectively, $p < 0.05$) were not as high as those for males (Table 4, Fig. 1). Regressions of foreleg length on body length were similar in that r^2 values were higher in males than in females; however, r^2 values for both sexes were considerably lower (0.39 for females and 0.61 for males, both $p < 0.05$) than those of the other legs. The slopes of the regression lines of middle leg length on body length and hind leg length on body length were significantly higher in males than in females ($t = 36.72$, $p < 0.001$, and $t = 29.89$, $p < 0.001$, respectively). There was no significant difference between the sexes in the slopes of the regression of foreleg length on body length ($t = 1.30$, $p > 0.1$).

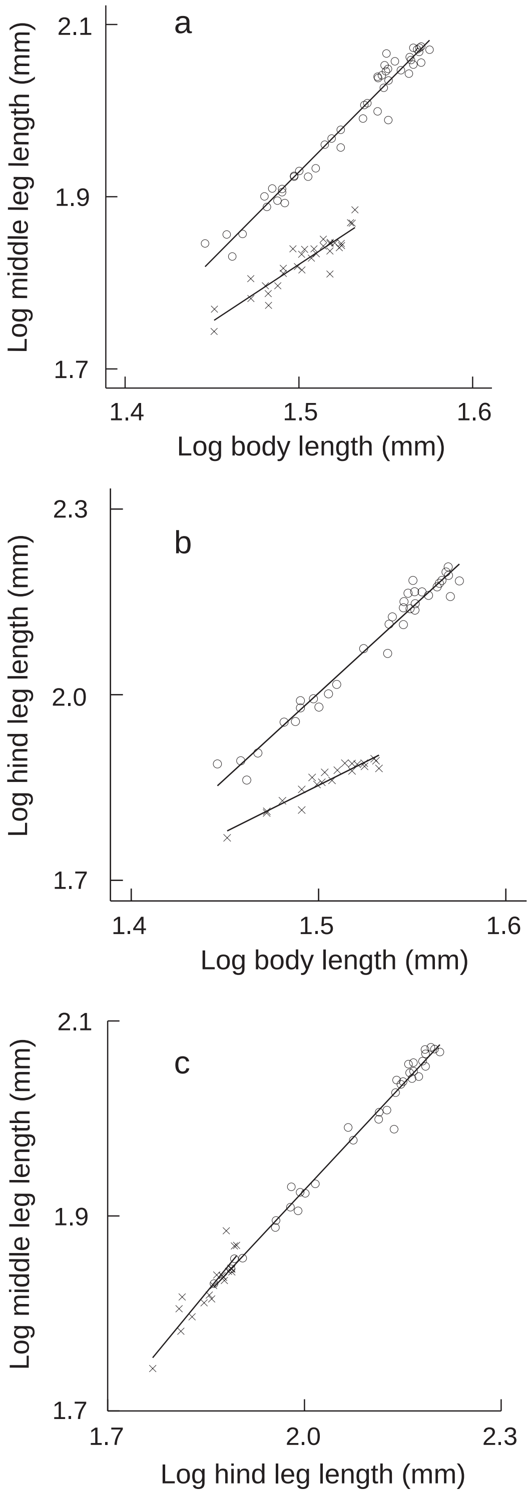
Body length accounts for much less of the variation in leg length components of *Ge. buenoi* than it does in *G. gigas*. Females' r^2 values ranged from 0.48 to 0.49 ($p < 0.05$), while males' r^2 values ranged from 0.26 to 0.31 ($p < 0.05$) (Table 5, Fig. 2). We refrained from specific tests of differences between slopes for males and females because there was little overlap in body lengths.

Leg ratios

The relationship between the middle and hind leg lengths in *G. gigas* can be characterized by regressing the two traits (Fig. 1). Log hind leg length is a good predictor of log middle leg length for both sexes ($r^2 = 0.82$ and 0.98 for females and males, respectively; $p < 0.05$ for both). The slopes of the regressions for both males and females are very similar (0.72 ± 0.02 (mean ± SE) for males and 0.91 ± 0.09 for females), and both are less than 1. Again there was too little overlap in the predictor variable to compare slopes statistically (Fig. 1).

A similar pattern is seen in the regressions of log middle leg length on log hind leg length for *Ge. buenoi* (Fig. 2). Log hind leg length is a good predictor of log middle leg length for both sexes of *Ge. buenoi* ($r^2 = 0.76$ and 0.72 for females and males, respectively; $p < 0.05$ for both). The

Fig. 1. Allometric relationships between leg-component lengths and body length for *Gigantometra gigas* (n = 34 males (○); n = 21 females (×)). (*a*) Log middle leg length on log body length. Males: $y = 2.05x - 1.14$; females: $y = 1.44x - 0.34$. (*b*) Log hind leg length on log body length. Males: $y = 2.82x - 2.23$; females: $1.59x - 0.53$. (*c*) Log middle leg length on log hind leg length. Males: $y = 0.72x + 0.47$; females: $y = 0.91x - 0.15$.



slopes of the regressions for males and females are very similar and are both less than 1 (0.89 ± 0.06 for males and 0.88 ± 0.05 for females) and fall within the range seen in *G. gigas*. These slopes do not differ significantly between the sexes ($t = 0.77$, $p < 0.2$).

Discussion

Although species of Gerridae typically exhibit female-biased SSD (Andersen 1982, 1997), careful examination of *G. gigas* reveals that all measured components of body size are significantly larger in males than in females. Our results contrast with the only other report for this species (unpublished data cited in Andersen 1997), where the ratio of female size to male size was given as 1.00. Although males appear to be larger than females in both *Aquarius elongatus* (Hayashi 1995) and *Limnoporus notabilis* (Fairbairn 1990) (two other species of Gerridae), this is the first report of male body length significantly exceeding that of females in this family. Our results also extend the general trend reported by Andersen (1982, 1997) that across species within the Gerridae, male body size increases at a faster rate than female body size. The body size of *Ge. buenoi* is more typical of the Gerridae, as is the fact that females are larger than males. The female size to male size ratio reported here for *Ge. buenoi* (1.19) is very close to that (1.11) reported by Andersen (1997).

Although the direction of this body size dimorphism in *G. gigas* is striking when compared with that in other gerrid species, the dimorphism in leg-component lengths is even more dramatic. The middle femur, middle tibia, and hind femur are all approximately 35% larger and the hind tibia is almost twice as long in males than females. In contrast, body length is, on average, only 1.1 times larger in males than in females. In short, at the small end of the male and female body size distribution, the sexes resemble each other in all dimensions, but at the large end, males have remarkably longer middle and hind legs, given a marginally greater body length. Andersen (1982) has suggested that *G. gigas* may be near the upper size limit for insects with this body plan, because the leg lengths required to support and propel a larger body may exceed the capacity of the skeletomuscular system. Our data suggest otherwise. Body length, in females at least, appears unconstrained. This is supported by the simple observation that for a given female body size, the leg lengths of like-sized males are considerable greater (Fig. 1). Thus, female size is not absolutely constrained by a supportable leg length.

Middle legs

The observation of strong sexual dimorphism in the allometric relationships between leg lengths and body length begs the question as to why the middle and hind legs of males are so large relative to their body size. The fact that there is sexual dimorphism argues against the proposition that these allometries act as any sort of strong constraint. Instead, adaptation by sexual selection of some sort is the natural, expected source. We have no observations of sexual behaviour in this species in the wild, and only a few in the laboratory (unpublished). Notably, we have observed that

Table 3. Sample sizes, means and standard deviations (SD), and coefficients of variation (CV) of leg-component lengths and body length for male and female *Gerris buenoi*, with the results of Student's *t* test for significant differences between the sexes (*n* is the sample size).

	Males				Females					
Length	Mean (mm)	SD (mm)	CV (%)	*n*	Mean (mm)	SD (mm)	CV (%)	*n*	*p*	Dimorphism (% difference)
Middle femur	4.70	0.17	3.6	63	4.94	0.19	3.8	92	<0.001	4.9
Middle tibia	3.70	0.14	3.8	63	3.99	0.18	4.5	92	<0.001	7.3
Total middle leg	11.26	0.4	3.6	63	12.01	0.49	4.1	92	<0.001	6.2
Hind tibia	4.39	0.18	4.1	63	4.57	0.18	3.9	92	<0.001	3.9
Hind femur	2.25	0.21	9.3	63	2.40	0.14	5.8	92	<0.001	6.3
Total hind leg	7.73	0.09	1.1	62	8.21	0.37	4.5	91	<0.001	5.8
Body	6.17	0.04	0.6	62	7.35	0.32	4.4	92	<0.001	16.1

Table 4. Results of the model II (geometric mean) regression analysis of total leg lengths and body lengths for *Gigantometra gigas*.

	log (*y*)	log (*x*)	Slope ± SE	y_{int} (mean ± SE)	r^2
Males	Foreleg length	Body length	1.09±0.12	–0.50±0.18	0.611
	Middle leg length	Body length	2.05±0.07	–1.15±0.11	0.960
	Hind leg length	Body length	2.82±0.09	–2.23±0.14	0.968
	Middle leg length	Hind leg length	0.72±0.02	0.47±0.04	0.983
Females	Foreleg length	Body length	1.17±0.21	–0.67±0.32	0.386
	Middle leg length	Body length	1.44±0.11	–0.34±0.16	0.894
	Hind leg length	Body length	1.59±0.12	–0.53±0.17	0.899
	Middle leg length	Hind leg length	0.91±0.09	–0.15±0.17	0.815

Note: All data are log-transformed from measurements in millimetres; all $p < 0.05$; standard errors are approximated from model I regression analysis; y_{int} is equal to the *y* intercept. See Methods for further details.

Table 5. Results of the model II (geometric mean) regression analysis of total leg lengths and body lengths for *Gerris buenoi*.

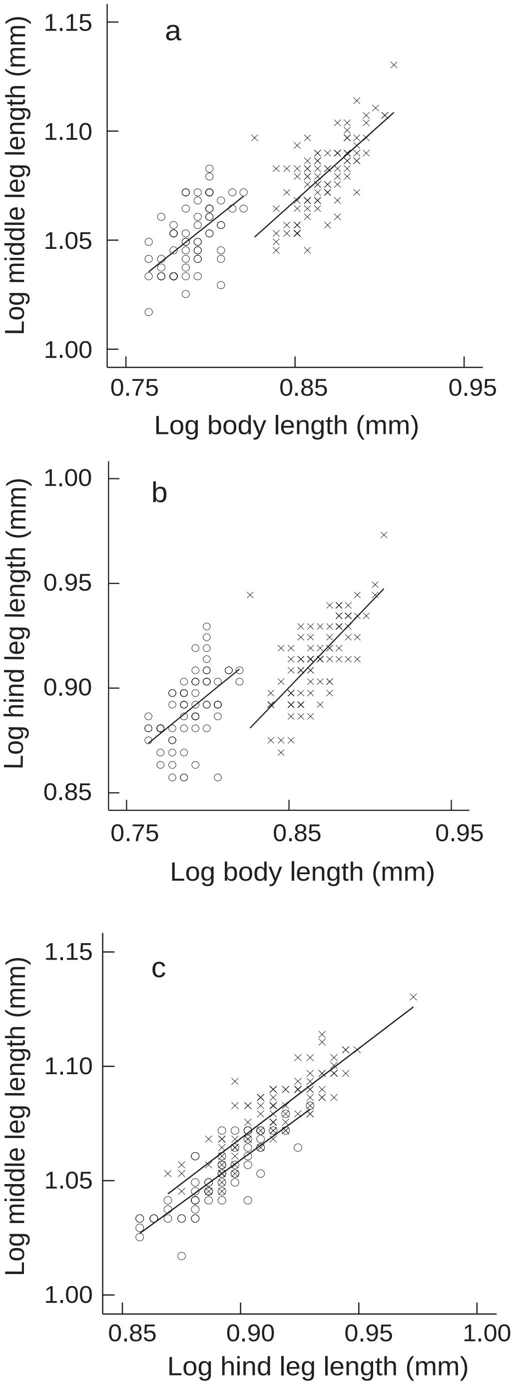
	log (*y*)	log (*x*)	Slope ± SE	y_{int} (mean ± SE)	r^2
Males	Middle leg length	Body length	1.11±0.11	0.18±0.09	0.312
	Hind leg length	Body length	1.24±0.14	–0.09±0.11	0.258
	Middle leg length	Hind leg length	0.89±0.06	0.26±0.05	0.717
Females	Middle leg length	Body length	1.00±0.08	0.21±0.07	0.475
	Hind leg length	Body length	1.13±0.09	–0.07±0.08	0.486
	Middle leg length	Hind leg length	0.88±0.05	0.27±0.04	0.761

Note: All data are log-transformed from measurements in millimetres; all $p < 0.05$; standard errors are approximated from model I regression; y_{int} is equal to the *y* intercept. See Methods for further details.

male *G. gigas* appear to harass other individuals by rapidly and vigorously thrusting their middle legs up- and downward on the water surface, with thrusts alternating between legs. These movements appeared much more aggressive than the surface signals common in some other gerrids (Andersen 1982; Spence and Andersen 1994; Arnqvist 1997). We do not know whether these actions are directed primarily toward males or females because our observations are few and we have seen the actions directed toward both sexes. Hayashi (1995) has noted a somewhat similar behaviour in another very large gerrid, *Aquarius elongatus*. Here, males fight with their middle legs, and Hayashi (1995) has detected sexual selection on the length of middle legs. Male *A. elongatus* have similarly long middle legs relative to females (Hayashi 1995). Finally, in other gerrids in which this allometry has been studied, and where no sexual selection on the middle legs is known, either there is no sexual dimorphism or it may even be reversed in sign (*Ge. buenoi* in this study; other species in Hayashi 1995).

The high phenotypic variance observed in the middle legs is typical of traits under directional sexual selection (Andersson 1994). High phenotypic variance may reflect genetic or phenotypic condition dependence of trait expression, both of which are expected to evolve under directional sexual selection (e.g. Price et al. 1993; Rowe and Houle 1996). We note that the patterns of allometry for the middle legs in both sexes of *G. gigas*, including the high variance in males, is nearly identical with that observed in another gerrid in which sexual selection on the middle legs is known to occur (Hayashi 1995). Similarly, in stalk-eyed flies the same patterns of allometry for eye-stalk length occurs in those species where eye-stalk length in males is under sexual selection (Wilkinson 1998). To verify our hypothesis, we require direct studies of sexual selection on the middle legs in

Fig. 2. Allometric relationships between leg-component lengths and body length for *Gerris buenoi*. (n = 62 males (○); n = 89 females (×)). (*a*) Log middle leg length on log body length. Males: $y = 1.11x + 0.18$; females: $y = 1.00x + 0.21$. (*b*) Log hind leg length on log body length. Males: $y = 1.24x - 0.09$; females: $y = 1.13x - 0.07$. (*c*) Log middle leg length on log hind leg length. Males: $y = 0.89x + 0.26$; females: $y = 0.88x + 0.27$.



G. gigas and studies of similar allometric relationships in closely related species in which the middle legs are not used in sexual interactions.

Hind legs

The sexual selection hypothesis, however, seems unlikely to directly account for the extreme sexual dimorphism in the allometric relationship between body length and hind leg length (Fig. 1). We have not observed the hind legs being used in any sexual interactions in *G. gigas*, unlike in *Rheumatobates rileyi* (Westlake et al. 1999). The hind legs of the Gerrinae appear to be used solely as rudders, acting during propulsive thrusts of the middle legs (Andersen 1982). We suggest that biomechanical constraints determine the relationship between the middle and hind legs, and any response of the middle legs to sexual selection can thereby be expected to lead to a correlated response in the hind legs. The close relationship between the middle and hind legs and the fact that it is relatively invariant between the sexes (Fig. 1) support this view. Moreover, in *Ge. buenoi*, where the middle legs are definitely not used in sexual interactions (Rowe 1992), the slopes of the relationship between the middle and hind legs for both sexes are quite similar to those in *G. gigas* (Fig. 2 and Results).

The rudder function of the hind legs is necessitated by unequal power strokes of the middle legs, which is the method by which Gerrinae turn (Andersen 1982). The tibial segments (the rudders) of the hind legs rest on the water surface behind, and in the same alignment as, the body. It is easy to see that as the middle legs increase in size, the torque generated by such unequal thrusts will require an elongated rudder (hind legs) to control. Observations of locomotion in the field (D.C. Currie, Royal Ontario Museum, personal communication) and our own observations in the laboratory suggest that the need for elongated hind legs to serve this rudder function may be particularly acute in *G. gigas*, which propels itself with single or multiple thrusts of the middle legs, one side at a time rather than both sides in unison as in other Gerrinae. Presumably this would greatly increase torque and therefore the need for elongated hind tibia. In support of this view, it is the length of the hind tibia that increases at the greatest rate with increases in body length and, therefore, with middle leg length in both male and female *G. gigas* (Table 2). Matsuda (1960) observed that the hind tibia are relatively long in the more primitive and larger genera. The role of mechanical constraints on this pattern is worth further examination.

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