SEXUAL DIFFERENCES IN BODY PROPORTIONS
OF *ZYGOBALLUS RUFIPES* PECKHAM AND PECKHAM
(ARANEAE, SALTICIDAE): AN EFFECT OF
CHELICERAL AND LEG ALLOMETRY

Dean B. Faber

Department of Zoology
University of Wisconsin-Madison
Madison, Wisconsin 53706

ABSTRACT

A suspected allometric relationship between chelicera length and body size in male *Zygoballus rufipes* was investigated. In order to minimize possible effects of geographic variation, all specimens available (24 males, 46 females) from a circumscribed area in south-central Michigan were studied. Power curve regressions of carapace width, carapace height, chelicera length, palp length, first leg length, and second leg length on a general measure of body size (carapace length) were calculated for each sex. The allometric relationship was expressed as $Y = b X^k$. In females all body measurements varied isometrically (linearly) with respect to carapace length (k = 0.91 - 1.04). In males chelicera length and first leg length were positively allometric with respect to carapace length (k = 1.43 and 1.44 respectively). The other male body measurements were all isometric with respect to carapace length (k = 0.96 - 1.04), with the exception of carapace width which was negatively allometric (k = 0.84). Tests of significance for differences between sexes in the slopes of the regression lines demonstrated significant differences for chelicera length (p < 0.10) and first leg length (p < 0.02). The allometric relationships of chelicera length and first leg length with carapace length in male *Z. rufipes* demonstrate a size dependent difference between sexes in body proportions (allomorphosis). This allomorphosis explains why sexual dimorphism is more pronounced among larger individuals of *Z. rufipes*.

INTRODUCTION

The term allometry encompasses a variety of different phenomena. Perhaps the most succinct recent definition is that of Gould (1977):

"allometry: change of shape correlated with increase or decrease in size. The change in size may reflect ontogeny, phylogeny, or merely the static differences among related individuals...".

A brief introduction to allometry is presented in Futuyma (1979). For more detailed discussions see Rensch (1960), Gould (1966, 1977), and Huxley (1972).

The present study is concerned with the variation within populations of adults of *Zygoballus rufipes* Peckham and Peckham and is a study of "... the static differences among related individuals...". This area of allometry has been variously referred to as allomorphosis (Simpson 1953, Gould 1966, 1977), size allometry (Mosimann 1970), and allometrie de taille (Teissier 1960). *Zygoballus rufipes* Peckham and Peckham 1885 is the senior synonym of *Zygoballus bettini* Peckham and Peckham 1888 (Edwards 1980).

Studies of size allometry (allomorphosis) in arthropods have been confined almost exclusively to the Insecta and Crustacea (see Oster and Wilson 1978, and Teissier 1960 respectively for detailed accounts). Within the Chelicerata, size allometry in Pycnogonida is discussed by Fry (1964) as an important complicating factor in numerical taxonomic analyses. Fisher (1977), based on experimental studies with models, concludes that prosomal spine allomorphosis in the carboniferous xiphosuran *Euproops danae* minimized lateral oscillations during settling behavior and thereby helped the animals to escape from predators. In addition Locket (1932, cited in Huxley 1972) reports on studies of cheliceral allometry in three species of spiders: *Theridion lineatum* and *T. instabile* (Theridiidae) and *Linyphia triangularis* (Linyphiidae). All three species show a positive cheliceral allometry in males and either isometry or a slight negative cheliceral allometry in females.

One of the distinguishing and frequently noted characteristics of the jumping spider genus *Zygoballus* is the presence of large, forward-directed chelicerae in males (Fig. 1, Peckham and Peckham 1909, Chickering 1944, Kaston 1948, 1978). Female *Zygoballus* have moderate-sized, downward-directed chelicerae (Fig. 2) such as are typical of both sexes in the great majority of Salticidae. This sexual dimorphism in the cheliceral morphology of *Zygoballus* is present only in adults. The characteristic chelicerae of the male are acquired at the final molt to maturity (Peckham and Peckham 1909). Cheliceral sexual dimorphism occurs in other salticid genera, of which *Salticus* and *Eris* are perhaps the best known examples (Kaston 1948). In addition to the enlarged chelicerae typical of the entire genus, the males of *Z. rufipes* also have much longer first legs relative to their overall size than do the females of this species (Peckham and Peckham 1889, 1909, Emerton 1891, Chickering 1944).

I am currently engaged in a revision of *Zygoballus* for the world. The examination of many specimens of *Z. rufipes* revealed that there was little sexual difference in chelicera and first leg length among small individuals of the same body size. However, among large individuals, males had disproportionately longer chelicerae and first legs than females of the same body size. Hence, allometric relationships between chelicera length and body size and between first leg length and body size were suspected.

The present study investigates the chelicerae, palpi, first and second legs, carapace width, and carapace height in both sexes of *Z. rufipes* for allometry with respect to carapace length. Carapace length was chosen as a general measure of body size because it is the largest linear dimension of the body which can be measured accurately. Total body length was not used because of the well known tendency of the abdominal dimensions of spiders to vary with the nutritional state of the individual.
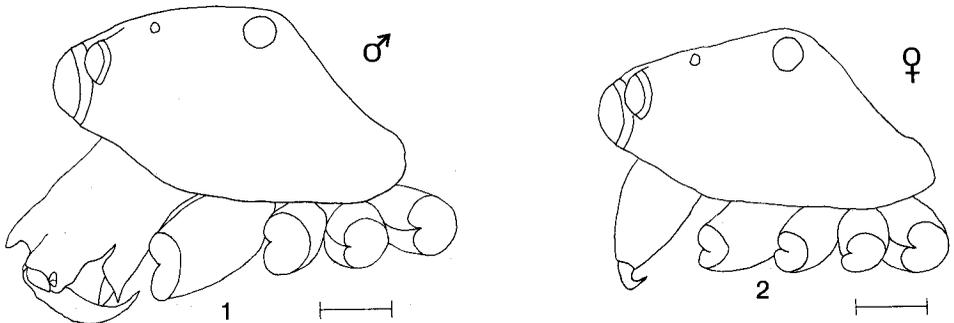
Figs. 1-2.—*Zygoballus rufipes* lateral views of the carapace: 1, male; 2, female. Scale lines equal 1 millimeter.

Table 1.–Descriptive statistics for seven body dimensions of *Zygoballus rufipes*, measured in millimeters.

		mean	standard deviation	coefficient of variation	range
carapace length	males	4.55	0.60	0.13	3.41 - 5.55
	females	4.29	0.25	0.04	3.84 - 4.89
carapace width	males	4.00	0.47	0.12	2.99 - 4.76
	females	3.72	0.23	0.06	3.29 - 4.45
carapace height	males	2.79	0.37	0.13	1.95 - 3.41
	females	2.40	0.17	0.07	2.13 - 2.74
chelicera length	males	2.46	0.50	0.20	1.46 - 3.17
	females	1.52	0.16	0.10	1.03 - 1.83
palp length	males	4.83	0.72	0.15	3.54 - 5.85
	females	3.70	0.30	0.08	3.23 - 4.39
first leg length	males	16.83	3.31	0.20	9.81 - 22.20
	females	10.85	0.78	0.07	8.90 - 12.56
second leg length	males	9.92	1.41	0.14	6.04 - 11.58
	females	8.35	0.63	0.07	7.07 - 9.69

In order to minimize the possible effects of geographic variation, the largest sample available from a single circumscribed geographical area was used (46 females and 24 males from an area in south-central Michigan).

MATERIALS AND METHODS

Specimens.–The specimens of *Z. rufipes* used in this study (24 males and 46 females) were collected from nine different localities in south-central Michigan. All specimens are adults collected by Arthur M. Chickering during 1930-1949 and are in the collection of the Museum of Comparative Zoology (MCZ). The collection localities all fall within a rectangle centered on Albion, Michigan and measuring 125 km. east to west and 55 km. north to south. The earliest day of the year of the nine different collection dates is April 27 and the latest is December 7.

Measurements.–Seven body dimensions of each spider were measured at 40x with an ocular micrometer (measurements of bilateral structures were made on the left side of the body). The body dimensions measured were: carapace length, maximum carapace width, maximum carapace height, chelicera length (measured from point of emergence from the carapace and not including the fang), palp length (less palpal coxa and trochanter), total first leg length (all seven segments), and total second leg length. Palp length, first leg length, and second leg length were sums obtained by adding individual limb segment lengths. The manner in which the carapace margin overlaps the insertions of the chelicera and palp makes it impossible to measure their total length without dismembering the specimens.

Statistical methods.–Descriptive statistics of the body dimensions (mean, range, standard deviation, and coefficient of variation) were calculated separately for each sex. After a logarithmic transformation, least squares linear regressions of the logs of each of the other six body dimensions on log carapace length were calculated for each sex. Linear

THE JOURNAL OF ARACHNOLOGY

Table 2.—Allometric regression of coefficients of *Zygoballus rufipes* for X and Y measured in millimeters where X = carapace length and Y = bX^k. p = level of significance of the differences between sexes in the slopes (k values) of the regression lines.

Y		k	p	b	r
carapace width	males	0.84	>0.15	1.12	0.96
	females	0.94		0.94	0.87
carapace height	males	0.96	>0.50	0.65	0.94
	females	0.91		0.64	0.73
chelicera length	males	1.43	<0.10	0.28	0.90
	females	1.04		0.33	0.55
palp length	males	1.04	>0.50	0.99	0.93
	females	0.97		0.90	0.69
first leg length	males	1.44	<0.02	1.88	0.91
	females	1.01		2.49	0.80
second leg length	males	1.04	>0.50	2.03	0.92
	females	0.95		2.10	0.73

correlation coefficients were also calculated using the transformed measurements for each of the other six body dimensions and carapace length. Tests of significance were performed for differences between sexes in the slopes of the regression lines for each body dimension regressed on carapace length. All of the above methods are discussed in detail in Steele and Torrie (1981).

RESULTS

Descriptive statistics for each of the seven body dimensions measured are shown in Table 1 and summarized graphically in Fig. 3. The mean, standard deviation, coefficient of variation, and range are larger in males for every body dimension studied. Note that the coefficients of variation for chelicera length and first leg length in males are particularly large.

The allometric regression coefficients and correlation coefficients for all regressions are shown in Table 2. In the females all body dimensions measured vary isometrically (linearly) with carapace length, with k values between 0.91 and 1.04. In the males chelicera length and first leg length vary with carapace length in a positively allometric fashion, with k values of 1.43 and 1.44 respectively. Carapace width, however, varies with carapace length in a negatively allometric fashion with a k value of 0.84. The other male body dimensions all vary isometrically with carapace length with k values between 0.96 and 1.04. A comparison of the allometric relationships for chelicera length for both sexes is shown graphically in Fig. 4. The results of tests of significance for differences between sexes in the slopes of the allometric regression lines are shown in Table 2. The slopes for regression lines are also shown in Table 2. The slopes for regressions of chelicera length and first leg length on carapace length are signficantly different between sexes at $p < 0.10$ (one tailed). The slopes for the other regressions are not significantly different between sexes, although those for carapace width are nearly significant at $p = 0.10$.

DISCUSSION

The presence of size allometry (allomorphosis) with respect to carapace length in the chelicera length and first leg length of male *Zygoballus rufipes* has been demonstrated in the sample studied. Tests of significance for sexual differences in the slopes of the allometric regressions of chelicera length and first leg length on carapace length indicate that the differences in the body proportions of larger members of the two sexes are a consequence of isometry in females and positive allometry in males.

While calculating the regression data for this study, I observed that the males collected during the summer months of July and August were consistently larger (as measured by carapace length) than those collected in either the spring (May and June) or fall (September and October). No such differences were apparent in females. This lead me to question whether there was a seasonal component to allometry in *Z. rufipes*. This hypothesis has been verified (Faber, in preparation).

The reasons for these sexual differences have not yet been clarified. The acquisition of enlarged chelicerae and first legs in male *Z. rufipes* at the final molt to maturity would suggest that male cheliceral and first leg allometry are connected with courtship display, male threat display, or some other aspect of adult behavior.

The Peckhams (Peckham and Peckham 1889) reported that two males of *Z. rufipes* "... displaying before one female rushed savagely upon each other and fought for 22 minutes, during one round remaining clinched for six minutes." Rovner (1969) reports similar behavior in *Linyphia triangularis*. Enlarged chelicerae would confer an obvious advantage in these "jousts."

In male *Z. rufipes* the first pair of legs are held above and to the sides of the body during courtship and threat displays (Peckham and Peckham 1889). It is possible that disproportionately long first legs may increase threat display and courtship success. If this is the case, then male cheliceral and first leg allometry would be consistent with Huxley's energy budget hypothesis (Huxley 1972). There may be a minimal total amount of energy required for a male to complete the life cycle. Beyond this amount however, reproductive success may be maximized by the allocation of as much energy as possible to the development of structures used in courtship and threat displays.
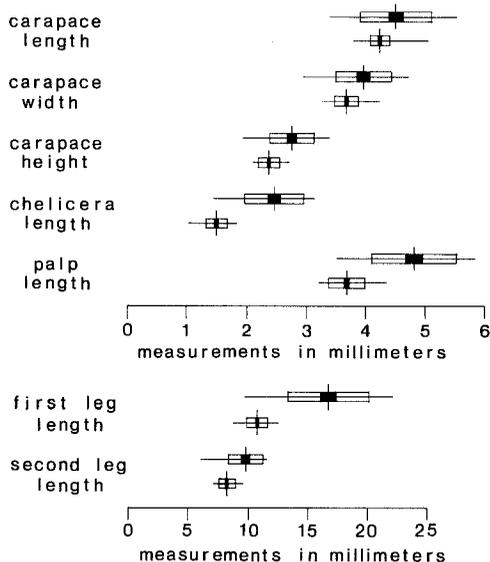

Fig. 3.–Graphical representation of descriptive statistics for all body dimensions measured for both sexes of *Zygoballus rufipes* (measurements in millimeters). The upper of each pair of symbols is for males, the lower is for females. Vertical line signifies means, horizontal line signifies range, unshaded bar signifies standard deviation, shaded bar signifies standard error of means.
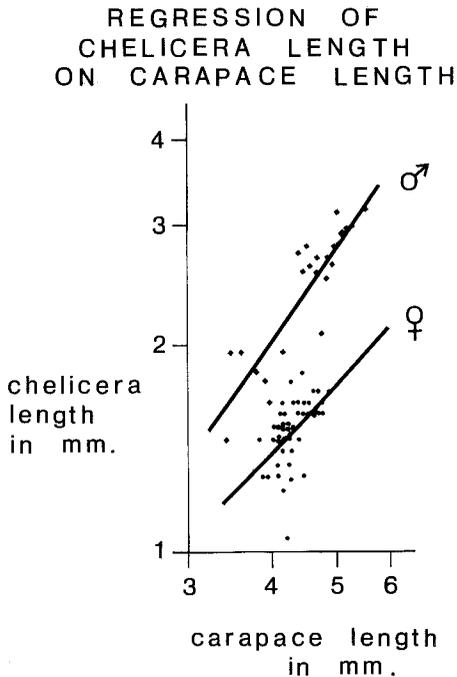
REGRESSION OF
CHELICERA LENGTH
ON CARAPACE LENGTH

Fig. 4.–Plot of the regressions of chelicera length on carapace length for both sexes of *Zygoballus rufipes*. Males designated by diamonds, females by circles.

    If fertile females are available for mating at all seasons, it may be that during periods of relative abundance of food, large males with disproportionately long chelicerae and first legs are more successful in mating with females, but during periods of food shortage there is little energy that can be allocated to the development of long chelicerae and first legs.

    The presence of positive cheliceral allometry in *Zygoballus rufipes* males increases to three (Salticidae, Theridiidae, and Linyphiidae) the number of spider families in which this phenomenon is known to occur. The hunting methods of *Zygoballus* are considerably different from those of *Linyphia* or *Theridion*. The presence in adult males only of positive cheliceral allometry in such phylogenetically distant and morphologically differ-ent families would suggest that there is a selection for this phenomenon which is inde-pendent of hunting strategy. Enhanced success in intermale aggressive display and fighting and consequent enhanced reproductive success may be the common factor selecting for positive cheliceral allometry in these three genera of spiders.

ACKNOWLEDGMENTS

LITERATURE CITED

Chickering, A. M. 1944. The Salticidae of Michigan. Papers Mich. Acad. Sci. Arts Lett., 29:139-222.
Edwards, G. B. 1980. Jumping Spiders of the United States and Canada: Changes in the Key and List. Peckhamia, 2(1):11-14.

Emerton, J. H. 1891. New England Spiders of the Family Attidae. Trans. Connecticut Acad. Arts Sci., 8:220-252.

Fisher, D. C. 1977. Functional Significance of Spines in the Pennsylvanian Horseshoe Crab *Euproops danae*. Paleobiology, 3(2):175-195.

Fry, W. B. 1964. The Pycnogonida and the Coding of Biological Information for Numerical Taxonomy. Syst. Zool., 13:32-41.

Futuyma, D. J. 1979. Evolutionary Biology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Gould, S. J. 1966. Allometry and Size in Ontogeny and Phylogeny. Biol. Rev., 41:587-640.

Gould, S. J. 1977. Ontogeny and Phylogeny. Belknap Press/Harvard University Press, Cambridge, Massachusetts.

Huxley, J. S. 1972. Problems of Relative Growth, 2nd ed. Dover Publications, Inc., New York.

Kaston, B. J. 1948. Spiders of Connecticut. Connecticut Geol. Nat. Hist. Survey, Bull. No. 70, Hartford, Connecticut.

Kaston, B. J. 1978. How to Know the Spiders, 3rd ed. Wm. C. Brown Co. Dubuque, Iowa.

Locket, G. H. 1932. Some Cases of Heterogonic Growth in Spiders. Ann. Mag. Nat. Hist., Ser. 10, 9:407-419.

Mosimann, J. E. 1970. Size Allometry: Size and Shape Variables with Characterizations of the Lognormal and Generalized Gamma Distributions. J. Am. Stat. Assoc., 65:930-945.

Peckham, G. W. and E. G. Peckham. 1889. Observations on Sexual Selection in spiders of the Family Attidae. Occasional Papers Nat. Hist. Soc. Wisconsin, 1:1-60.

Peckham, G. W. and E. G. Peckham. 1909. Revision of the Attidae of North America. Trans. Wisconsin Acad. Sci. Arts Lett., 16:355-646.

Rensch, B. 1959. Evolution Above the Species Level. English Translation of 2nd German ed., Columbia University Press, New York.

Rovner, J. S. 1968. Territoriality in the Sheet-Web Spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Z. Tierpsychol., 25:232-242.

Simpson, G. G. 1953. The Major Features of Evolution. Columbia University Press, New York.

Steele, R. G. D. and J. H. Torrie. 1981. Principles and Procedures of Statistics 2nd ed., McGraw-Hill Book Co., New York.

Teissier, G. 1960. Relative Growth. Pp. 537-560, *in:* The Physiology of the Crustacea, T. H. Waterman (ed.). Academic Press, London, vol. 1.