2012. The Journal of Arachnology 40:338–344

Static allometry and sexual size dimorphism in *Centruroides margaritatus* (Scorpiones: Buthidae)

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Abstract. Animal body traits are scaled relative to overall body size depending on the evolutionary context. Most naturally selected traits are scaled approximately isometrically (constitute a constant proportion of the body size at different body sizes), whereas those under sexual selection tend to present positive static allometry (be proportionally larger in larger individuals). However, there are body traits that might be influenced by both natural and sexual selection. We studied the courtship behavior of the scorpion *Centruroides margaritatus* (Gervais 1841) and analyzed the static allometry of several body traits. We hypothesized that those traits that were actively used in courtship and seemed to be sexually dimorphic could be under sexual selection. The main sexually dimorphic traits were body size (female larger) and metasoma length (male longer). Although metasoma length of males had a steeper allometric slope (larger males had longer metasoma) than that of females, the slopes did not differ significantly. All body traits measured showed isometry with body size, except that the pecten presented negative allometry in males. Thus the length of the metasoma of males, thought to be influenced by sexual rather than natural selection, did not present positive allometry as expected. Males used the metasoma actively while courting females.

Keywords: Courtship behavior, isometry, sexual selection, natural selection

Variation in the size and shape of particular body parts relative to variation in body size at a given life stage (static allometry) is generally thought to be the result of either sexual selection or natural selection (Darwin 1879; Andersson 1994; Emlen 2008). If a male morphological feature has evolved as a weapon in fights with other males, a positive allometric relationship is predicted (Huxley 1932; Schroeder & Huber 2001; Kodric-Brown et al. 2006) (but see Eberhard 2002; Bondurianski & Day 2003). In this context, larger males would have proportionally larger weapons than smaller males ($b > 1$ in a log-log regression of size of a given structure on body size). This is because individuals with larger weapons usually have an advantage in resolving direct male-male battles (Eberhard & García-C 1999; Eberhard et al. 2000; Schroeder & Huber 2001). Thus, positive allometry should be expected in secondary sexual characters under strong intrasexual selection. However, male genitalia, which are thought to evolve under intersexual sexual selection (Eberhard 1985, 1996), nearly always have negative allometry ($b < 1$) (Eberhard 2008). This may be expected if it is advantageous for males to have "standard sized genitalia" that would fit the most common size of females in the population according to the 'one-size-fits-all' hypothesis (Eberhard et al. 1998). Alternatively, such a standard size in genitalia may be more efficient to transfer sperm: a natural selection role (House & Simmons 2003).

The relative size of traits in which both sexual and natural selection forces are involved is less predictable. Traits under the exclusive influence of natural selection are expected, at least in most cases, to have isometric relationships with body size (b equal to or nearly equal to 1, Eberhard et al. 2009), though this is not always the case (see Klingenberg & Zimmermann 1992). It is common in a wide range of animal species that legs, antennae, wings, horns, and other structures are used in the context of both natural and sexual selection (Eberhard 1996, 2004, 2010). For instance, in a large number of spider species adult males not only use their legs (particularly leg I) and chelicerae to court their mates (Stratton et al. 1996; Eberhard & Huber 1998; Barrantes 2008; Aisenberg & Barrantes 2011), but also as walking and killing and feeding organs, respectively. Hence, given the dual or multiple functions of a trait subject to the combined action of natural and sexual selection, the type of allometric relationship is difficult to predict. In these cases, a more reliable approach to evaluate the effect of sexual and natural selection on particular body parts relative to body size is to compare the relative magnitude of the slopes across traits between sexes (Eberhard et al. 2009). In addition, this approach allows using different body features as controls for one another (Rodríguez & Al-Wathiqui 2012).

The courtship behavior of scorpions includes a series of tactile and vibratory stimuli produced with parts of the male's body that are used in both sexual and non-sexual contexts (Polis & Sissom 1990; Lourenço 2000). Typically, the courtship in scorpions is roughly divided into four phases: initiation, promenade a deux, sperm transfer and termination (Polis & Farley 1979; Tallarovic et al. 2000). Detailed descriptions of all these phases for different species can be found in Polis and Sissom (1990) and Lourenço (2000). Some male behaviors occur in more than one phase, while others are restricted to only one. For instance, shaking and rocking the body back and forth while standing immobile (juddering), and spreading out the pectines, often sweeping the substrate with them, occur in most phases. In contrast, the male contacting the female with his metasoma and sting ("sexual sting") and using the metasoma to club the female occur only during the initiation phase (Polis and Sissom 1990). The male grasping of the chelae of the female with his own to guide her during the dance and cheliceral massages occurs during both the promenade a deux and sperm transfer. The use of multiple body parts in the courtship behavior (and in other non-sexual functions) of scorpions is convenient for examining how the size of these body parts change in relation to change in body size.

Our study has a twofold objective: to complement the description of the courtship behavior of *Centruroides margaritatus*

(Gervais 1841) (family Buthidae) provided by Briceño and Bonilla (2009), and to analyze the sexual dimorphism and allometric relationships of those body traits involved in the courtship behavior of *C. margaritatus*. In addition we include other traits that are not directly involved in the courtship behavior (e.g., leg IV) as well as female morphological traits in the allometric analysis for comparative purposes. We expect a positive allometric relationship (or at least a steeper slope) for the length of male metasoma since this structure is longer in adult males than in females, despite the smaller size of males, and it is used actively during courtship. Considering a possible effect of sexual selection, we also expect a steeper slope for male traits relative to the same female traits and for male traits involved in courtship relative to those that are not.

METHODS

Courtship behavior.—We video-recorded the courtship behavior of one adult pair of *C. margaritatus* (collected by E. Arévalo, at Atenas, Alajuela Province; 9°58′N, 84°26′W; 1013 m elevation) to obtain a detailed description of the different behaviors involved in courtship as a baseline to select the morphological traits to measure. The female and male were housed individually in plastic containers: 24.3 cm length, 14.3 cm width, 6.8 cm height for the female's container and 13.7 cm, 12.8 cm, 5 cm for the male's container. We covered the bottom of each container with approximately 2 cm of sand and placed a small rock near a corner of the female's container to provide a suitable surface on which the male could deposit the spermatophore. During captivity scorpions were offered crickets (*Acheta domesticus*) twice a week and water ad libitum.

Material examined.—We measured the area, width and length of the carapace, length and width of the chela, segments of the metasoma, telson, pecten, and patella of legs I and IV of 25 adult males and 19 adult females in the Arachnological Collection of the Museo de Zoología, Universidad de Costa Rica that were collected in different localities of the Central Valley and northwestern region of Costa Rica: UCR 7 (1 ♀), UCR 8 (1 ♀), UCR 20 (1 ♀), UCR 21 (1 ♀), UCR 24 (1 ♀), UCR 31 (1 ♀), UCR 33 (1 ♀, 2 ♂), UCR 36 (1 ♀), UCR 49 (1♂), UCR 53 (1 ♀), UCR 66 (1 ♂), UCR 86 (1 ♂), UCR 163 (1 ♂), UCR 164 (1 ♀), UCR 183 (1 ♀), UCR 187 (1 ♂), UCR 188 (1 ♀), UCR 189 (1 ♂), UCR 190 (1♀, 1 ♂), UCR 193 (1 ♂), UCR 195 (1 ♀), UCR 197 (1 ♀), UCR 201 (1 ♂), UCR 211 (3 ♂), UCR 212 (1 ♀, 3 ♂), UCR 213 (1 ♂) ,UCR 215 (2 ♂), UCR 214 (1 ♀), UCR 218 (1 ♀), UCR 220 (1 ♀, 2 ♂), UCR 223 (3 ♂). We photographed each body part under a dissecting microscope using a Nikon Coolpix 4500 camera and then measured the different body parts using the program UTHSCSA Image Tool v. 2.1.

Statistical analyses.—We examined the effect of sex on size variability of several different body parts using a Multivariate Analysis of Variance (MANOVA). We then correlated the square root of the area, width and length of the carapace (males: $r = 0.99$, $P < 0.000001$, same value for area vs. width and length of carapace males; females: $r = 0.91$, $P < 0.00001$, and $r = 0.92$, $P < 0.00001$ for width and length of female's carapace respectively), and selected the carapace area as a measure of body size as all three variables are highly correlated. Although width and length of the carapace are frequently used as a measure of body size, its area is less prone to variation in length or width of the carapace (Gonzaga & Vasconcellos-Neto 2001). Next, we determined the relationship between change in body size (carapace area) and the size of each body part using regression analyses and analyses of covariance (ANCOVA) to compare slopes of each variable between both sexes. Then we compared the slopes, b, obtained from regressing the carapace area against each of the other variables between sexes, using a paired *t*-test. Though slopes calculated for each variable are independent between sexes, we used a paired *t*-test rather than a *t*-test for independent samples because this approach allows us to evaluate if in general the morphological features of a particular sex are larger (in proportion to the body size) than in the other sex. We chose ordinary least squares regression (OLS) over reduced major axis regression (RMA) for the following reasons: OLS describes the functional relationship (cause-effect) between variables; it distinguishes the effect of one variable on the other from the individual variation; it is very robust to variation of the error in x and does not underestimate slope values as had previously been argued (Al-Wathiqui & Rodríguez 2011). We used the R Statistical Language (version 2.14: http://cran.r-project.org) for all statistical analyses and $\log_{10}$ transformed all variables prior to regression analyses.

RESULTS

Courtship behavior.—A few seconds after the male had been placed in the female cage, she walked a few steps toward the male. As soon as the male detected her (possibly by substrate vibrations), he started to judder, rocking his abdomen rapidly dorso-ventrally. At the same time he spread his pectines outward and downward, moving them forward and backward, sweeping the ground. The female walked toward the male, coiling her metasoma over her midline. She often moved her metasoma down and to one side for a few seconds, raising it again as she approached the male. The male also moved forward toward her, juddering nearly continually. Once he got close, he seized the patella of her left pedipalp with his right pedipalp, and then moved his left pedipalp and grasped her right chela. At the same time the female maintained her metasoma coiled and tilted toward one side. Often she slightly uncoiled its basal segments, extending them toward the male, but she kept the fifth segment and the telson coiled. She also swept the ground with her pectines, but less frequently than the male.

Once the male had grasped the female's chelae, he began to move forward, pushing the female backward. He then switched and began to walk rapidly backward, pulling the female toward him, holding her chelae. He continued to sweep the ground with his pectines. This stage is described as the promenade a deux (Polis & Farley 1979). On several occasions the female briefly resisted the male's pulls; in response he juddered and pulled her toward him by the chelae. If the female still resisted, the male juddered again, apparently with more intensity, and extended his first legs, contacting the base of female's pectines and rubbing them with a more or less circular movement of his tarsi.

Several times during the promenade a deux phase the pair walked over a rock, and sometimes the female stopped on top of it. The male beat the rock surface rapidly with alternate

Table 1.—Mean (mm) and standard deviation (SD) of morphological variables for males and females and statistical (ANOVA) comparisons.

Variable	Mean male	SD male	Mean female	SD female	$F_{(1/42)}$	P
Carapace area	7.13	1.18	7.94	1.28	4.60	0.0378
Carapace length	7.94	1.33	8.83	1.33	4.65	0.0369
Carapace width	7.58	1.20	9.07	1.44	13.73	0.0006
Chela width	3.08	0.54	3.66	0.82	6.98	0.0115
Pincer length	7.94	1.33	8.83	1.40	0.98	0.3272
Metasoma seg. 1	8.51	1.85	6.86	1.29	9.57	0.0035
Metasoma seg. 2	10.49	2.35	8.47	1.42	9.33	0.0039
Metasoma seg. 3	11.48	2.61	9.09	2.61	10.91	0.0019
Metasoma seg. 4	11.82	2.49	9.65	1.72	9.24	0.0041
Metasoma seg. 5	12.09	2.41	10.18	1.83	7.19	0.0104
Metasoma length	54.39	11.56	44.25	7.85	9.35	0.0039
Telson length	6.57	1.32	5.96	0.98	2.34	0.1333
Pecten length	7.70	1.24	7.38	1.30	0.73	0.3961
Patella leg I	4.40	0.72	4.67	0.72	1.18	0.2842
Patella leg IV	7.24	1.41	7.48	1.48	0.29	0.5949

movements of his first legs (drumming, hereafter), and the female responded to this behavior by lifting her abdomen dorsally, allowing the male to rub her pectines as described above.

The promenade a deux is thought to allow the male to search for a suitable surface on which to deposit his spermatophore (Polis & Farley 1979). The male pulled the female to the rock more than eight times; the last time she stayed still for several seconds almost in the middle of the rock. The male immediately began to move his pedipalps alternately up and down, while grabbing female's chelae with his own chelae. The movements of his pedipalps became faster and simultaneous rather than alternate, as he deposited his spermatophore. Immediately afterward, the female moved forward and the male started drumming the rock with his first legs. The female continued moving forward, while the male grabbed her chelae.

The male then drummed, uncurled and extended his metasoma forward (leaving the telson curled), reaching the anterior, dorsal section of the female metasoma. It appeared as if he were trying to strike her with the posterior end of his metasoma. During this struggle she freed herself from his pedipalps, turned her body ca. 180°, and clubbed the male with the posterior end of her metasoma while he was juddering. Then she walked about 10 cm from the male. The male approached her but she clubbed him twice with her metasoma and he moved away.

The video-recordings showed that the up-and-down fast movements of the male pedipalps occurred while the male was extruding his spermatophore. It was also evident from the video that a thread-like structure connected the spermatophore to the male opercula after it was attached to the rock, and that the spermatophore changed from a nearly horizontal position to a vertical position when the male walked toward the female. At the end the female moved away without accepting the spermatophore.

Morphometric analysis.—A significant amount of the combined variance of all morphological variables was explained by differences between sexes (MANOVA: Pillai test = 0.89, *df* = 15/28, $P < 0.000001$). All three measures of the carapace (area, length, and width) were significantly larger in females than in males (Table 1). The width but not the length of the chelae was greater in females than males (Table 1). Each segment of the metasoma, and consequently the total length of the metasoma, was longer in males than females (Table 1). The lengths of the telson, pecten and patellae of legs I and IV did not differ significantly between males and females (Table 1).

All morphological variables of males and females increased with body size (carapace area) (Fig. 1, Table 2A). Metasoma segments, particularly segments 1 and 2, and total metasoma length increased faster with body size in males than in females, but slopes did not differ significantly between sexes for any of these variables, based on pairwise comparisons (Table 2A). The width and length of the chelae, as well as the other body parts (the lengths of the telson and of leg patella I and IV) also showed similar increments with body size for both males and females (Table 2A, Fig. 1). However, slopes calculated for morphological features of males were overall significantly larger than those calculated for the same features in females (paired *t*-test: 3.21, *df* = 10, $P = 0.008$), indicating that in relation to body size, body parts of males increased faster (except for pecten length and chela width, Table 2A). All body parts scaled isometrically ($b = 1$) on body size, except for the length of the pecten in males. Pecten length in males differed in having a negative allometry (Table 2A, Fig. 1). The slope for patella IV vs. patella II showed an isometric relationship for females, but a positive allometry for males (Table 2B).

DISCUSSION

The courtship and sperm transfer of *C. margaritatus* is very stereotyped. With the exception of two behaviors, the contact of the anterior section of the female pectines with the tarsus of male first legs and the movement of the male pedipalps during the spermatophore extruding, the courtship of *C. margaritatus* is very similar to the courtship of many other species (Polis & Sissom 1990; Lourenço 2000). We documented the contact of female pectines in two other species of *Centruroides* (*C. bicolor* Pocock 1898, *C. limbatus* Pocock 1898: C. Sánchez-Quiroz unpubl. data), and Lourenço (2000) described the same behavior in *Tityus fasciolatus* (Pessa 1935). We also documented the movement of the male pedipalp during spermatophore extrusion in these two other *Centruroides* species (C. Sánchez-Quiroz unpubl. data), suggesting that both of these

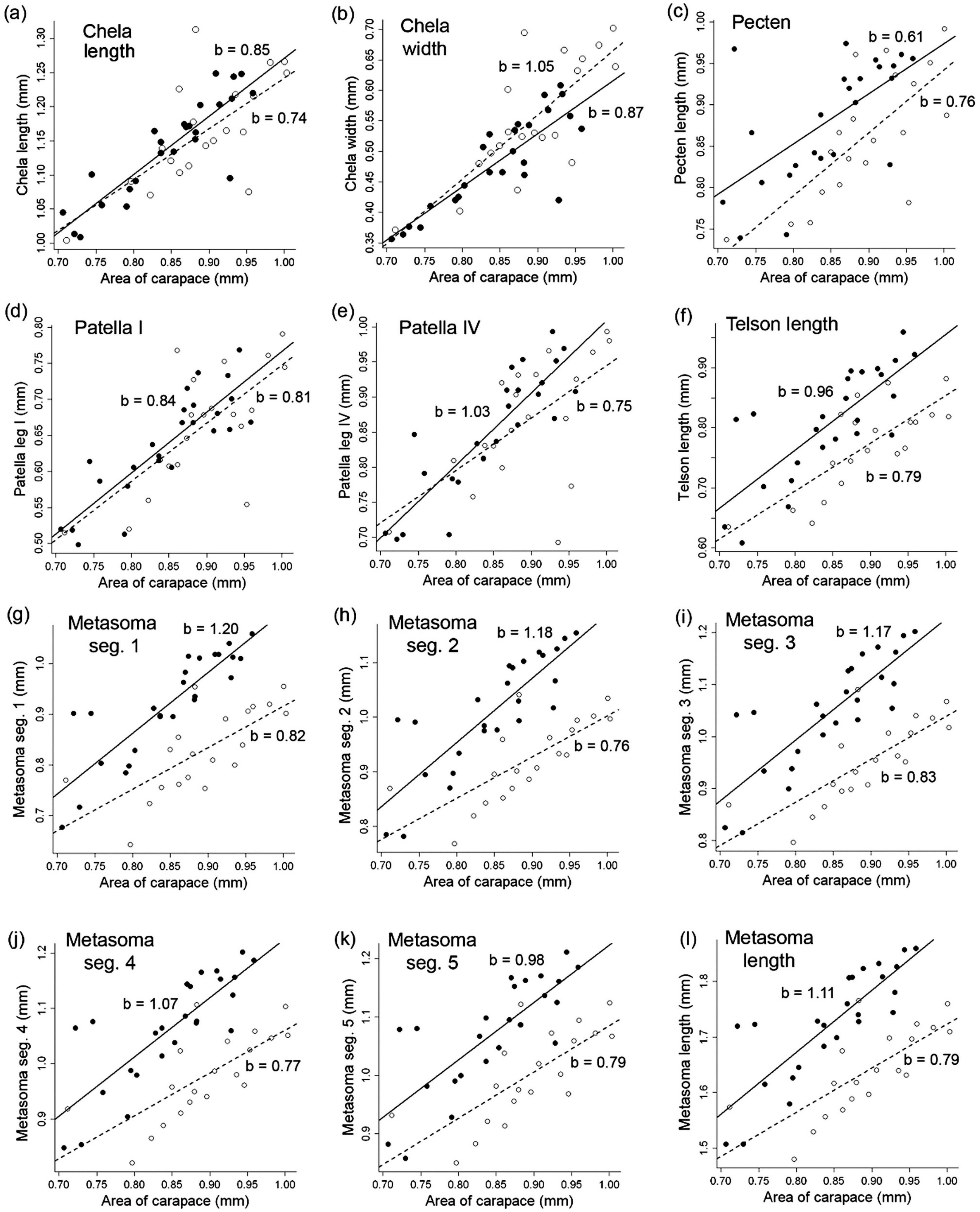

Figure 1.—Relationship of the square root of the carapace area to the other 12 morphological traits. The continuous line and black circles correspond to the area of the carapace of males regressed against each of the other morphological traits, and the dashed line and empty circles correspond to the area of the carapace of female regressed against each of the other morphological traits. Slope values for males and females are included. All variables were $\log_{10}$-transformed.

Table 2.—Allometric relationship between different morphological variables, with the square root of carapace area as a measure of body size. It includes *F*-test for the slope (H_0: b = 0), the slope value, the proportion of the variance of each dependent variable explained by carapace area (r^2) for males and females and a $P_{(\text{bm-bf})}$ value of the comparison between male-female slopes. All variables were $\log_{10}$-transformed. Negative allometry is indicated by *, and positive allometry by **.

	Males				Females				
Variable	$F_{(1/23)}$	b	r^2	*P*	$F_{(1/18)}$	b	r^2	*P*	$P_{(\text{bm-bf})}$
A, carapace area (independent variable)									
Chela width	57.39	0.87	0.71	< 0.00001	27.31	1.05	0.60	0.00006	0.41
Chela length	80.83	0.85	0.78	< 0.00001	16.36	0.74	0.48	0.00076	0.58
Metasoma seg. 1	70.45	1.20	0.75	< 0.00001	18.54	0.82	0.51	0.00042	0.11
Metasoma seg. 2	55.07	1.18	0.70	< 0.00001	21.87	0.76	0.55	0.00019	0.07
Metasoma seg. 3	48.09	1.17	0.68	< 0.00001	24.89	0.83	0.58	0.00009	0.16
Metasoma seg. 4	43.47	1.07	0.65	< 0.00001	19.06	0.77	0.51	0.00037	0.22
Metasoma seg. 5	37.13	0.98	0.62	< 0.00001	20.34	0.79	0.53	0.00027	0.44
Metasoma length	51.81	1.11	0.69	< 0.00001	21.58	0.79	0.54	0.00020	0.17
Telson length	36.01	0.96	0.61	< 0.00001	27.38	0.79	0.60	0.00006	0.45
Pecten length	14.61	0.61*	0.40	0.0009	19.91	0.76	0.52	0.00030	0.51
Patella leg I	63.66	0.84	0.73	< 0.00001	17.88	0.81	0.50	0.00050	0.86
Patella leg IV	71.26	1.03	0.76	< 0.00001	10.58	0.75	0.37	0.00441	0.25
B, patella IV (independent variable)									
Patella leg I	399.6	1.17**	0.95	< 0.00001	36.26	0.88	0.67	< 0.0001	0.07

behaviors are also widespread among the New World Buthidae.

Sexual size dimorphism is notable between females and males of *C. margaritatus*. Body size of females (considering the area of the carapace as an index of body size) is larger than the body size of males. This is a general pattern in scorpions (Polis & Sissom 1990) and is an expected consequence of the different reproductive role played by each sex (Williams 1966; Prenter et al. 1998). In arthropods, the reproductive success of females is directly related to body size, and larger females are capable of carrying either larger number of eggs (or embryos) or larger eggs (or embryos) (Andersson 1994), though evolution of sexual size dimorphism has possibly been influenced by many different factors rather than only by differences in reproductive role (Hormiga et al. 2000; Barrantes 2008). Females of *C. margaritatus* also have more robust (wider) chelae. The size of the chelae varies in scorpions between sexes and across genera (Meijden et al. 2009). In *Centruroides* and other genera (e.g., *Heterometrus*, *Isometrus*), females have more robust chelae, but the opposite pattern is found, for example, in *Buthus* and *Scorpio* (Polis & Sissom 1990). Sexual differences in the dimensions of the chelae are expected to be related to different diet and size of prey captured or differences in the use of chelae in courtship behavior. However, there is not enough information on scorpions to separate the effects of diet and courtship on the morphological design of the chelae (Polis 1979; McCormick & Polis 1990; Benton 1992).

Males of *C. margaritatus* are smaller than females but have longer metasomas, and in general body parts increase faster (relative to body size) than in females. Presumably, male *C. margaritatus* reach adulthood one molt earlier than females, as occurs in *C. gracilis* (Latreille 1804) (Franke & Jones 1982), and the smaller size in males is thus a direct consequence of their early maturation. An early maturation may provide males with the advantage of an early breeding start relative to females and a greater maneuverability that may allow them to decrease predation risk (Andersson 1994). On the other hand, the difference in the length of the metasoma is manifested only in adult scorpions (Polis & Sissom 1990; Lourenço 2000); in previous stages length of metasoma is similar in both males and females. This seems to be a general pattern in scorpions, though no data are available for *C. margaritatus*. It is likely that the longer metasoma in males is the result of a faster growth rate (acceleration: Reilly et al. 1997). In contrast, the size of females may increase more gradually, since they have one more molt (hypermorphosis, Reilly et al. 1997). Since males have a longer metasoma, and this feature is present only during adulthood and the metasoma is used in male-female sexual interactions, it is expected that the longer metasoma in adult males is related to its sexual role.

With the exception of the length of the pecten, which had a negative allometric relationship, all other morphological features of *C. margaritatus* had a proportional change relative to body size (b = 1). It is often stated that traits evolved under sexual selection have a positive allometry (b > 1) relative to body size, based on the assumption that larger individuals benefit more in allocating more resources to the growth of the selected trait than small individuals (Huxley 1932; Gould 1974; Green 1992; Kodric-Brown et al. 2006). However, the cost and benefit of producing and carrying proportionally larger structures likely varies both among different traits and among different species (Eberhard 2002; Bonduriansky & Day 2003). The balance between cost and benefit in producing and carrying sexually selected traits, and the counterbalancing effect of sexual selection and natural selection acting on the same trait, may yield relationships between the size of a trait and body size that differ from positive allometry, converting the absolute value of 1.0 to an unreliable indicator of the existence or absence of sexual selection (Bonduriansky & Day 2003). In fact, positive allometry seems to be the exception and not the rule for traits used by males as weapons and signaling devices that evolved through sexual selection (Bonduriansky & Day 2003; Bonduriansky 2007). Thus, the isometry of different traits in *Centruroides* that are thought to have evolved under sexual selection follows the more general trend (even scaling of a trait on body size) found in many other species (Eberhard 2002; Bonduriansky & Day 2003; Bonduriansky 2007). The positive allometry of patella I relative to patella IV in males, but their isometric relation in females, supports the argument that body structures under sexual selection can scale differently on body size. In this case both patellae are homologous, but the patella IV is used as a control (Eberhard et al. 2009; Rodriguez & Al-Wathiqui 2012), since sexual selection is expected to affect patella I but not patella IV (see description of courtship behavior).

The even scaling of nearly all traits on body size in *C. margaritatus* may be related to the function of such body parts and the counteracting effect of sexual and natural selection on the same traits. It is possible that body parts used as tactile signaling devices (e.g., tarsus I, chelae) have a more or less "standard size" that is appropriate for stimulating most females in the population (mean female size) (W. Eberhard unpubl. information). In many other arthropods, selection favoring standard non-genital contact structures (e.g., genital clasping structures) tends to result in isometry or even negative allometry (Eberhard 1996, 2004, 2010). Thus, each of the structures used by male *C. margaritatus* to stimulate females in a specific area may be also under stabilizing selection, similar to the genital clasping structures. A similar scaling pattern between body parts and body size in *C. margaritatus* may result from the balanced effects of natural and sexual selection acting on the same trait (Bonduriansky & Day 2003). For instance, if longer first legs are more suitable for stimulating females but have a negative effect on survival, the balanced effect of both sexual and natural selection may result in an even scaling of leg I on body size. Hence, the interaction of the natural and sexual selection (Elgar & Fahey 1996), as well as the selection for standard size of non-genital contact structures (Eberhard 2004, 2010), likely affects the shape and design of some body parts in male *C. margaritatus*, acting as stabilizing forces that result in a proportional size of these body parts relative to the body size.

ACKNOWLEDGMENTS

We thank William Eberhard, Rafael L. Rodríguez and two anonymous reviewers for their comments and suggestions on previous versions of this manuscript, and William Eberhard for allowing us access to an unpublished manuscript. This investigation was partially supported by the Vicerrectoría de Investigación, Universidad de Costa Rica.

LITERATURE CITED

Aisenberg, A. & G. Barrantes. 2011. Sexual behavior, cannibalism, and mating plugs as sticky traps in the orb weaver spider *Leucauge argyra* (Tetragnathidae). Naturwissenschaften 98:605–613.

Al-Wathiqui, N. & R.L. Rodríguez. 2011. Allometric slopes not underestimated by ordinary least squares regression: a case study with *Enchenopa* treehoppers (Hemiptera: Membracidae). Annals of the Entomological Society of America 104:562–566.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Barrantes, G. 2008. Courtship behavior and copulation in *Tengella radiata* (Araneae, Tengellidae). Journal of Arachnology 36:606–608.

Benton, T.G. 1992. Determinants of male mating success in a scorpion. Animal Behaviour 43:125–135.

Bonduriansky, R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution 61:838–849.

Bonduriansky, R. & T. Day. 2003. The evolutionary of static allometry in sexually selected traits. Evolution 57:2450–2458.

Briceño, R.D. & F. Bonilla. 2009. Substrate vibrations in the scorpion *Centruroides margaritatus* (Scorpiones: Buthidae) during courtship. Revista Biología Tropical 57 (Suppl. 1):267–274.

Darwin, C. 1879. The Descent of Man and Selection in Relation to Sex. Murray, London.

Eberhard, W.G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Massachusetts.

Eberhard, W.G. 1996. Female control. Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.

Eberhard, W.G. 2002. Natural history and behavior of *Chymomyza mycopelates* and *C. exophthalma* (Dipetera: Drosophilidae), and allometry of structures used as signals, weapons, and spore collectors. Canadian Entomologist 134:667–687.

Eberhard, W.G. 2004. Male-female conflict and genitalia: failure to confirm predictions in insects and spiders. Biological Reviews 79:121–186.

Eberhard, W.G. 2008. Static allometry and animal genitalia. Evolution 63:48–66.

Eberhard, W.G. 2010. Rapid divergent evolution of genitalia. Theory and data updated. Pp. 161–223. *In* The Evolution of Primary Sexual Characters in Animals. (J.L. Leonard & A. Córdoba-Aguilar, eds.). Oxford University Press, New York.

Eberhard, W.G. & B.A. Huber. 1998. Courtship, copulation and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. Journal of Arachnology 26:342–368.

Eberhard, W.G. & J.M. García-C. 1999. Ritual jousting by horned *Pamsoschoenus expositus* weevils (Coleoptera, Curculionidae, Baridinae). Psyche 103:55–84.

Eberhard, W.G., J.M. Garcia-C & J. Lobo. 2000. Size-specific defensive structures in a horned weevil confirm a classic battle plan: avoid fights with larger opponents. Proceedings of the Royal Society of London B 267:1129–1134.

Eberhard, W., R.L. Rodríguez & M. Polihronakis. 2009. Pitfalls in understanding the functional significance of genital allometry. Journal of Evolutionary Biology 22:435–445.

Eberhard, W.G., B.A. Huber, R.L. Rodríguez, R.D. Breceño, I. Salas & V. Rodríguez. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. Evolution 52:415–431.

Elgar, M.A. & B.F. Fahey. 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). Behavioral Ecology 7:195–198.

Emlen, D.J. 2008. The evolution of animal weapons. Annual Review of Ecology Evolution and Systematics 39:387–413.

Francke, O.F. & S.K. Jones. 1982. The life history of *Centruroides gracilis* (Scorpiones, Buthidae). Journal of Arachnology 10:223–239.

Gonzaga, M.O. & J. Vasconcellos-Neto. 2001. Female body size, fecundity parameters and foundation of new colonies in *Anelosimus jabaquara* (Araneae, Theridiidae). Insectes Sociaux 48:94–100.

Gould, S.J. 1974. The origin and function of 'bizarre' structures: antler size and skull size in the "Irish elk", *Megaloceros giganteus*. Evolution 28:191–220.

Green, A.J. 1992. Positive allometry is likely with mate choice, competitive display and other functions. Animal Behaviour 43: 170–172.

Hormiga, G., N. Scharff & J.A. Coddington. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). Systematic Biology 49:435–462.

House, C.M. & L.W. Simmons. 2003. Genital morphology and fertilization success in the dung beetle *Onthophagus taurus*: an example of sexually selected male genitalia. Proceedings of the Royal Society of London B 270:447–455.

Huxley, J.S. 1932. Problems of Relative Growth. John Hopkins University Press, Baltimore, Maryland.

Klingenberg, C.P. & M. Zimmermann. 1992. Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. American Naturalist 140:601–620.

Kodric-Brown, A., R.M. Sibly & J.H. Brown. 2006. The allometry of ornaments and weapons. Proceedings of the National Academy of Sciences 103:8733–8738.

Lourenço, W.R. 2000. Reproduction in scorpions, with special reference to parthenogenesis. Pp. 71–85. *In* Proceedings of the 19th European Colloquium of Arachnology. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus, Denmark.

McCormick, S. & G.A. Polis. 1990. Prey, predators and parasites. Pp. 294–320. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

Meijden, A.V.D., A. Herrel & A. Summers. 2009. Comparison of chela size and pincer force in scorpions; getting a first grip. Journal of Zoology 280:319–325.

Polis, G.A. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionidae: Vaejovidae). Journal of Zoology 188:333–346.

Polis, G.A. & R.D. Farley. 1979. Behavior and ecology of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae). Journal of Arachnology 7:33–46.

Polis, G.A. & W.D. Sissom. 1990. Life history. Pp. 161–223. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

Prenter, J., W.I. Montgomery & R. Elwood. 1998. No association between sexual size dimorphism and life histories in spiders. Proceedings of the Royal Society of London B 265:57–62.

Reilly, S.M., E.O. Wiley & D.J. Meinhardt. 1997. An integrative approach to heterochrony: the distinction between interspecific and intraspecific phenomena. Biological Journal of the Linnaean Society 60:119–143.

Rodríguez, R.L. & N. Al-Wathiqui. 2012. Causes of variation in sexual allometry: a case study with the mating signals and genitalia of *Enchenopa* treehoppers (Hemiptera Membracidae). Ethology, Ecology and Evolution 24:187–197.

Schroeder, L. & R. Huber. 2001. Fight strategies differ with size and allometric growth of claws in crayfish, *Orconectes rusticus*. Behaviour 138:1437–1449.

Stratton, G.E., E.A. Hebets, P.R. Miller & G.L. Miller. 1996. Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 24:186–200.

Tallarovic, S.K., J.M. Melville & P.H. Brownell. 2000. Courtship and mating in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). Journal of Insect Behavior 13:827–837.

Williams, G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton, New Jersey.

Manuscript received 1 April 2012, revised 13 August 2012.