

Sexual Dimorphism in Functional Response and Trophic Morphology in *Rabidosa rabida* (Araneae: Lycosidae)

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ABSTRACT.—We investigated sexual dimorphism in feeding behavior and morphological characteristics associated with prey capture in the wolf spider, *Rabidosa rabida* (Araneae, Lycosidae). Female *R. rabida* attack and consume more prey than do males. In addition to behavioral differences between males and females, morphological features such as chelicerae size and venom gland size are also larger in females. These morphological differences are significant even after accounting for their positive correlation with body size. These data suggest that differences between the sexes in the relationship between fitness and foraging result in a dichotomy between male and female foraging behavior and differences in morphology associated with prey capture.

INTRODUCTION

Differences between the sexes are evident in a wide variety of organisms and numerous hypotheses have been proposed to explain the evolution of these differences (Shine, 1989; Hedrick and Temeles, 1989; Andersson, 1994; Reynolds and Harvey, 1994; Fairbairn, 1997). Sexual selection, intersexual niche divergence and differences in reproductive roles are the three most prominent hypotheses that have been used to explain the evolution of sexual dimorphism in size or in various other morphological characteristics (*e.g.*, Darwin, 1871; Shine, 1989; Hedrick and Temeles, 1989; Andersson, 1994; Reynolds and Harvey, 1994). While all of the above hypotheses are plausible and are known to operate in natural populations, determining the exact mechanisms which have resulted in sexual dimorphism is difficult (Hedrick and Temeles, 1989).

Sexual dimorphism in feeding ecology and morphological features associated with feeding have been documented in a number of organisms (*e.g.*, Selander, 1966; Carothers, 1984; Shine, 1989, 1991, 1993; Vaudry *et al.* 1990; Shine *et al.*, 1996a, b). These differences have been used as the primary evidence for intersexual niche divergence; however, they can also result from differences in reproductive roles, or sexual selection (Selander, 1972; Shine, 1989; Hedrick and Temeles, 1989; Temeles and Roberts, 1993). In many cases a combination of different selection pressures may result in sexual dimorphism in trophic characteristics (Anderson and Vitt, 1990; Temeles and Roberts, 1993; Perry, 1996; Herrell *et al.*, 1999). For instance, in some species of lizard sexual dimorphism in head size simultaneously results in an advantage in intrasexual interactions and allows for resource partitioning between the sexes (Anderson and Vitt, 1990; Bull and Pamula, 1996; Preest, 1994).

Spiders have long been recognized as a premier example of sexual size dimorphism (*e.g.*, Darwin, 1871; Elgar, 1991; Vollrath and Parker, 1992, 1997; Head, 1995; Coddington *et al.*,

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1997; Vollrath, 1998; Prenter *et al.*, 1997, 1998, 1999; Hormiga *et al.*, 2000). In most species of spider females are the larger sex and are considered sedentary egg producers whereas males are considered active searchers that roam the landscape to find females (Vollrath and Parker, 1992; Foelix, 1996). These differences in lifestyle are correlated with differences in feeding behavior between male and female spiders. For instance, in many web-building species, only adult females build webs to capture prey whereas males may not build a web at all and generally feed rarely after maturity (Foelix, 1996).

Females are larger than males in nonweb building spiders, but they are generally less dimorphic than web-building species (Vollrath and Parker, 1992; but see Coddington *et al.*, 1997; Prenter *et al.*, 1997, 1998, 1999; Hormiga *et al.*, 2000). In nonweb building species both males and females must physically overwhelm prey. Thus, measuring differences between males and females in foraging behavior is not complicated by the presence of a web in females and its absence in males. Existing data on the foraging behavior of these spiders are consistent with the hypothesis that females are selected to be more effective predators than males (Haynes and Sisojevic, 1966; Hardman and Turnbull, 1974; Givens, 1978; Moring and Stewart, 1992). However, it is not clear if there are differences only in behavior or if there are corresponding differences in the size of morphological features associated with prey capture (*i.e.*, chelicerae and venom glands).

The goal of this study was to relate sexual dimorphism in prey capture ability in a cursorial spider species, *Rabidosa rabida* (Walckenaer) (Aranaea, Lycosidae), to differences in the morphology of the trophic apparatus. As an indication of differences in foraging performance, we quantified the functional response, or the response of an organism to different densities of prey, of males and females separately. We then measured their body size and the size of structures involved in prey capture (the chelicerae and venom glands) to test the hypothesis that sex differences in trophic morphology are related to sex differences in foraging.

METHODS

Rabidosa rabida (hereafter referred to as *Rabidosa*) is a large wolf spider which inhabits old fields in tall grass or weeds (Dondale and Redner, 1990; Brady and McKinley, 1994). *Rabidosa* are agile, capable of rapid locomotion and generally do not build burrows (Brady and McKinley, 1994). Females are approximately 10% larger than males based on carapace width measurements from our population (S. E. Walker, pers. obs.). We chose this species because the behavior patterns used in prey capture as well as the morphological features critical to prey capture (chelicerae and the venom apparatus) have been described (Rovner, 1980).

Male and female *Rabidosa* were collected from Miami University's Ecology Research Center (Butler Co., Oxford Ohio) in June and July of 1996 and 1997. In 1996 we characterized the functional response of male and female *Rabidosa* by monitoring the number and proportion of prey captured at different prey densities (N = 21 Females, N = 27 Males). In 1997 spiders were collected and preserved in 70% ethanol for later analysis of morphological characteristics associated with prey capture (N = 17 Females, N = 8 Males).

In the laboratory spiders were maintained in clear cylindrical containers 8.5 cm in diameter by 14.5 cm high in an incubator on a 14:10 L:D cycle at 25 C with 60–70% relative humidity. The containers had 3–5 cm of mulch on the bottom, which was kept damp, and the spiders were fed at least once weekly. In preparation for feeding experiments, spiders were fed to satiation with crickets (*Acheta domesticus*) and then starved for two weeks to standardize hunger levels. Male and female spiders were randomly assigned to the following range of prey densities: 1, 2, 4 or 8 50–100 mg crickets. At the designated time the crickets

were introduced into the container and the spider was allowed to forage. After 24 h the number of prey killed (remains cannot be found and remains evident) and the number still alive were recorded.

The number of prey killed was square root transformed to meet assumptions of ANOVA and then analyzed using a two-factor ANOVA (sex and initial prey density). To determine the type of functional response, we used logistic regression to model the proportion of prey killed across prey densities (Juliano, 1993). Differences between males and females in the proportion of prey killed were determined by using indicator variables included in the logistic regression model (Collet, 1991).

Morphological characteristics of males and females were measured (± 0.05 mm) using a dissecting microscope equipped with an ocular micrometer. Carapace width was used as an indicator of body size. This has been proposed as the best linear estimate of spider size and has been used throughout the literature as an indicator of spider size (*e.g.*, Hagstrum, 1971; Marshall and Gittleman, 1994; Jakob *et al.*, 1996). Each chelicera is made up of two segments, a large basal segment referred to as the paturon and a smaller distal segment that is the fang (Kaston, 1981). Measurements were made on a randomly chosen chelicera, either the left or right. Width was measured at the widest point of the paturon and length was measured from the base of the paturon to the point where the fang articulates at the outer corner of the paturon. Fang width was measured where the fang attached to the paturon. Venom glands were removed from the spider by first removing the carapace and then dissecting out the venom gland's. Venom gland size was estimated by removing the venom gland and measuring the length of the venom gland from the base of the paturon and the width of the venom gland was measured at its widest point. While other morphological features are important in prey capture (*e.g.*, leg spination and scopular hairs, Rovner, 1980) it was felt that separating the effects of sexual selection acting on these characters would be difficult in this species since the legs are used in the courtship display and have some ornamentation (*see* Hebets and Uetz, 2000). Sex differences in trophic characteristics were examined using an analysis of covariance with cephalothorax width as the covariate. ANCOVA was used to account for differences in body size between the sexes. In each case the specific morphological characteristic of interest was the dependent variable and sex was the independent variable with carapace width as the covariate.

RESULTS

The number of prey killed increased with prey density (Fig. 1a, $F_{(3,40)} = 19.09$, $P < 0.001$) and females killed more prey than did males (Fig. 1a, $F_{(1,40)} = 11.63$, $P = 0.002$). There was no significant sex by density interaction ($F_{(3,40)} = 0.64$, $P = 0.611$) which demonstrates there was constant difference between male and female spiders regardless of density. However, the proportion of prey killed was not related to initial prey density (Fig. 1b, $\chi^2 = 0.02$, $df = 1$, $P = 0.898$). The proportion of prey killed was significantly higher for females than for males (Fig. 1b, $\chi^2 = 18.32$, $df = 1$, $P < 0.001$). Since there was no significant interaction between sex and prey density ($\chi^2 = 0.008$, $df = 1$, $P = 0.930$) indicating the same relationship between prey density and the proportion of prey killed for both males and females, the parameters of the logistic regression were estimated using a model which did not include the sex and prey density interaction (Table 1).

Cephalothorax width, paturon length and width, fang width and venom gland length and width were generally larger in females than in males (Table 2). Trophic characteristics were all positively correlated with cephalothorax width in both males and females (Table 2). ANCOVA with cephalothorax width as the covariate indicated that the width of the fang, and the length and width of the paturon were significantly larger in females than males

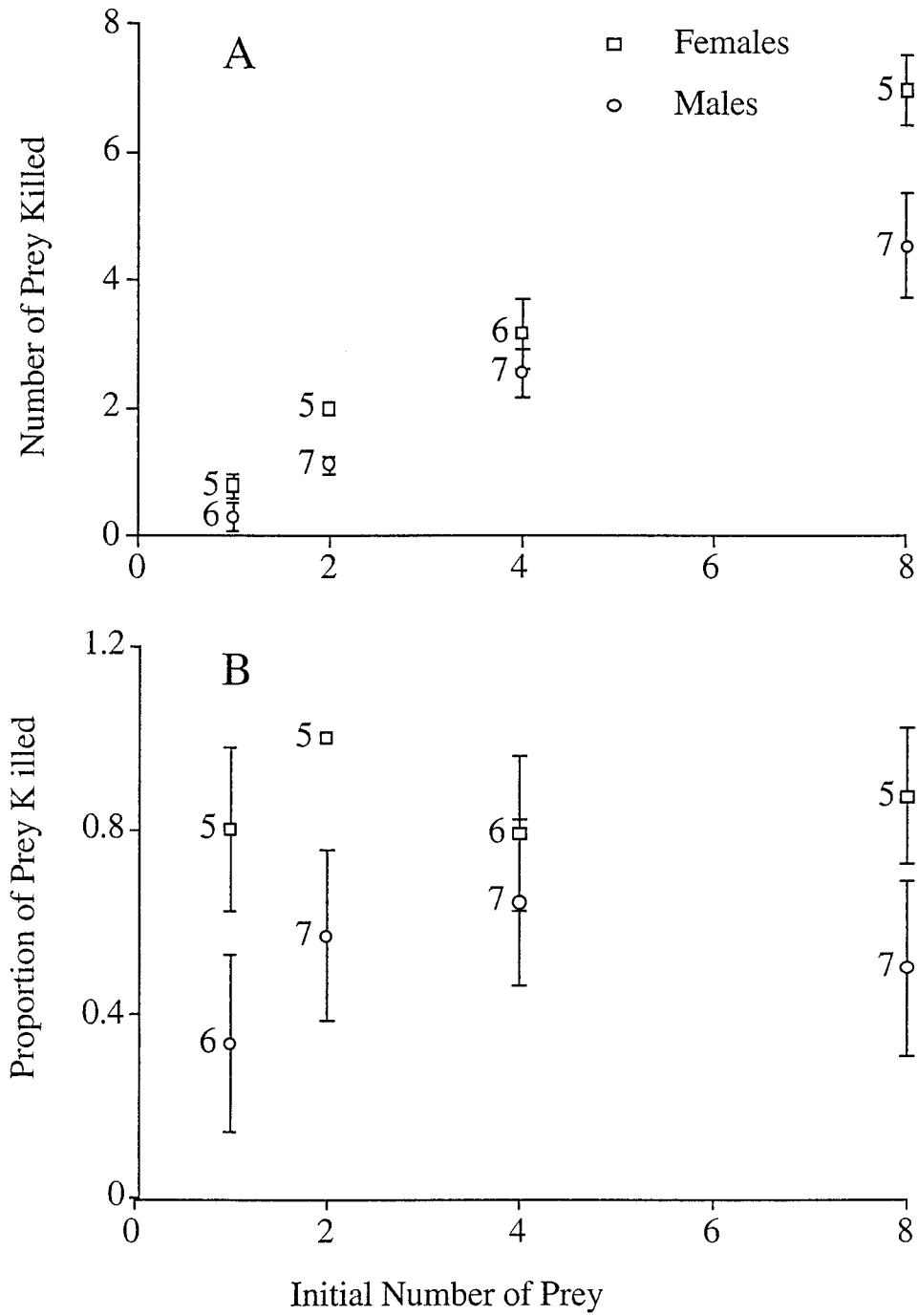


FIG. 1.—The effect of initial prey density and sex on the number of prey killed (A) and the proportion of prey killed (B). Data are shown as means \pm 1 SE. The sample size for each sex prey density combination are shown next to each point

TABLE 1.—Results of a Logistic Regression Model to determine the relationship between the proportion of prey killed, sex and initial prey density. Sex was coded as 0 if male and 1 if female

Parameter	DF	Estimate	Standard error	χ^2	P
Intercept	1	0.220	0.421	0.273	0.601
Prey Density	1	0.016	0.065	0.059	0.808
Sex	1	1.151	0.381	15.78	<0.001

after accounting for differences in body size (Fig. 2a–c: Fang Width $F_{(1,22)} = 62.6$, $P < 0.001$, Paturon Length $F_{(1,22)} = 105.35$, $P < 0.001$, Paturon Width $F_{(1,22)} = 100.14$, $P < 0.001$). Analysis of the length and width of the venom glands yielded similar results. After removing the effects of size, the length and width of venom glands was significantly greater in females when compared to males (Fig. 3a, b: Venom Gland Length $F_{(1,14)} = 28.30$, $P < 0.001$, Venom Gland Width $F_{(1,14)} = 42.82$, $P < 0.001$).

DISCUSSION

Most studies which have investigated sex differences in trophic morphology in spiders have focused on exceptional species in which male chelicerae are much larger than the females (Jackson, 1982, 1986; Pollard, 1994) and these differences appear to be a result of intrasexual competition rather than niche divergence (Rovner, 1968; Jackson, 1982; Faber, 1984). Interestingly, the modification of the chelicerae for male-male combat in some Salticids actually results in reduced foraging ability for males (Jackson, 1982, 1986; Pollard, 1994). Our data show that female *Rabidosia* captured and killed more crickets than did males across all densities and the morphological characteristics associated with prey capture were proportionately larger in females than in males when a measure of spider size, carapace width, was taken into account. Since male chelicerae size is smaller, the differences in trophic morphology between male and female *Rabidosia rabida* are more indicative of intrasexual niche divergence or differences in the reproductive roles of males and females than sexual selection.

TABLE 2.—Mean, N and SE of cephalothorax width, paturon length, paturon width, width of fang, venom gland length and venom gland width. The Pearson correlation between cephalothorax width and each characteristic is also reported (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$)

Characteristic	Sex	N	Mean \pm SE (mm)	t-test comparing males and females	Correlation with cephalothorax width
Cephalothorax width	Female	17	5.33 \pm 0.09	$t = 2.26$,	—
	Male	8	4.93 \pm 0.09	$P = 0.034$	—
Paturon length	Female	17	3.50 \pm 0.10	$t = 6.78$,	0.80****
	Male	8	2.62 \pm 0.10	$P < 0.001$	0.89***
Paturon width	Female	17	1.39 \pm 0.02	$t = 8.93$,	0.61**
	Male	8	1.04 \pm 0.03	$P < 0.001$	0.93***
Fang width	Female	17	0.52 \pm 0.01	$t = 7.85$,	0.54*
	Male	8	0.38 \pm 0.02	$P < 0.001$	0.81*
Venom gland width	Female	10	1.05 \pm 0.03	$t = 7.70$,	0.62
	Male	7	0.67 \pm 0.05	$P < 0.01$	0.61
Venom gland length	Female	10	4.37 \pm 0.20	$t = 4.88$,	0.93****
	Male	7	3.10 \pm 0.19	$P = 0.002$	0.96****

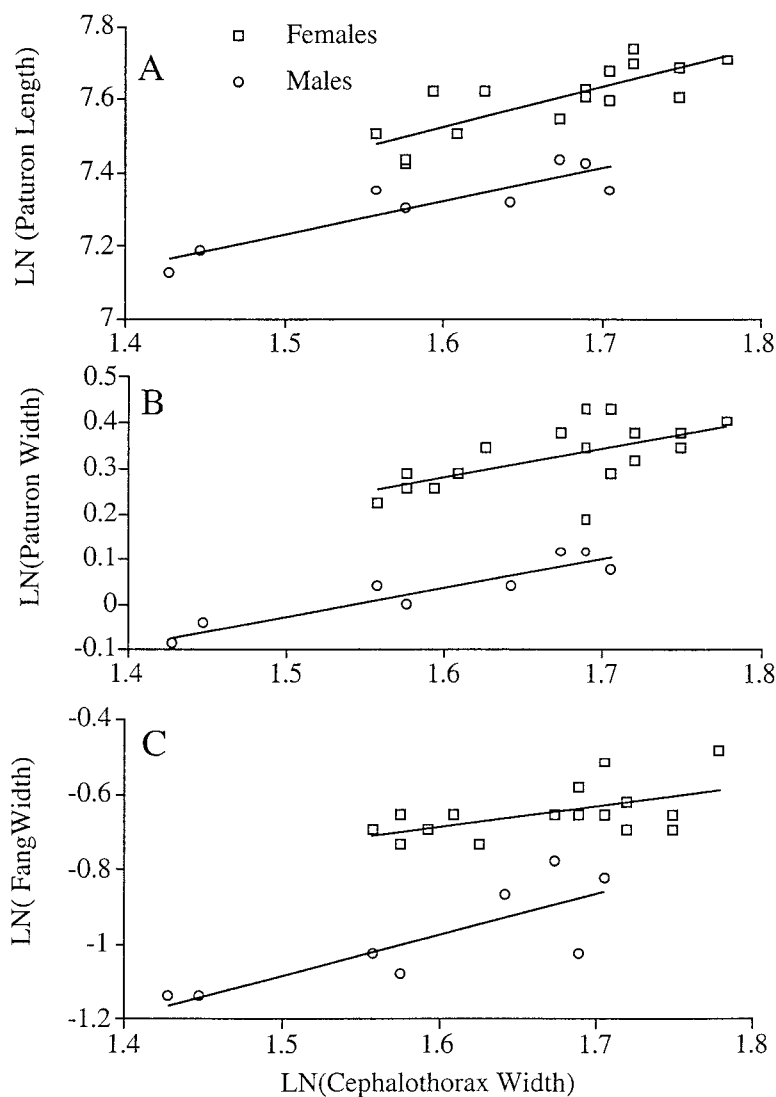


FIG. 2.—Relationship between paturon length (A), paturon width (B), fang width (C) and cephalothorax width. For illustration, the line from a least squares regression is shown for each sex

In many species of spider a direct link has been established between food consumption and the number of eggs produced by a female (*see* Wise, 1993) while there is little, if any, evidence that there is a strong link between adult male food consumption and fitness, except survival. For females increased foraging success results in more eggs (*see* Wise, 1993). Males are generally more active than females (Hallander, 1967; Hardman and Turnbull, 1974) which reflects their need to maximize time spent searching for mates and minimize time spent foraging (Givens, 1978). This has led to the characterization of males as time minimizers, organisms that attempt to spend as little time foraging as possible. Females are

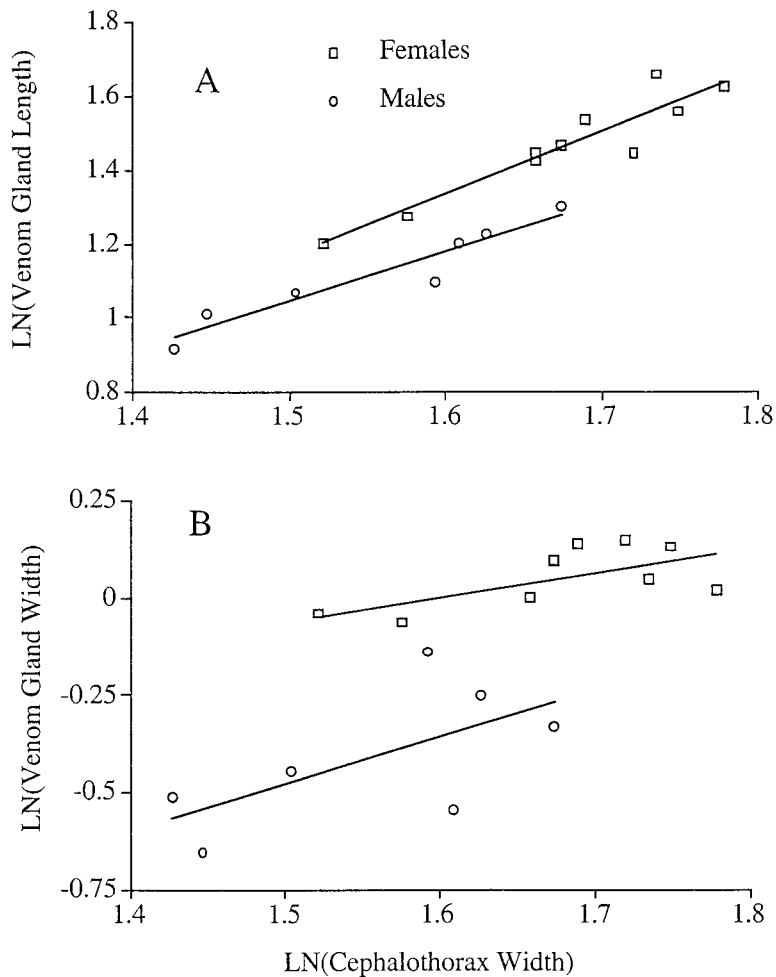


FIG. 3.—Relationship between venom gland length (A), venom gland width (B) and cephalothorax width. For illustration, the line from a least squares regression is shown for each sex

characterized as energy maximizers, organisms that attempt to consume as much as possible and thus maximize energy intake (Schoener, 1971). Our data show that females are more likely to consume a large number of prey compared to males under similar conditions which supports the hypothesis of males as time minimizers and females as energy maximizers.

The type of functional response generally exhibited by spiders is a type 2 response where the number of prey captured approaches an asymptote hyperbolically as prey density increases (Riechert and Harp, 1987; Wise, 1993). A type 1 functional response (number of prey killed increases linearly) is considered unrealistic because it suggests that predators are not limited by handling time or that they never become satiated and stop feeding (Gotelli, 1995). Over the prey densities that we observed, the response was linear in both males and females. However, given that we measured the response over a narrow range of prey densities using small prey, this result is not surprising. We selected small prey items so

they could be easily attacked and consumed by both males and females, thus minimizing the effects of prey size on differences in functional response. However, in doing this we limited the effects of handling time and satiation resulting in a linear functional response.

The size of the chelicerae and venom apparatus are important for prey capture in *Rabidosa* (Rovner, 1980). Both the chelicerae and fangs are used to restrain prey while the venom apparatus is needed to immobilize prey before ingestion (Rovner, 1980). Female *Rabidosa* have proportionally larger venom glands and chelicerae than males. Larger chelicerae and fangs might allow females to attack and consume larger prey than males. While there is little published evidence that females capture larger prey than males (*see* Givens, 1978), it seems logical to speculate that they might. In particular, larger venom glands would facilitate the use of more venom on more dangerous or larger prey. Spiders do inject more venom in larger prey or difficult to capture prey (Perret, 1977; Pollard, 1990; Boeve, 1994; Boeve and Meir, 1994; Boeve *et al.*, 1995). Also, since evidence suggests that venom regenerates slowly (Perret, 1977; Boeve, 1994; Boeve and Meir, 1994), larger venom glands would allow females to take advantage of the presence of multiple prey items. Thus, the differences here between males and females would allow females to take a wider variety of prey as well as a larger number of prey than males.

While differences in trophic structures in a variety of taxa have been suggested as good evidence of competitive niche divergence between males and females (Selander, 1966; Shine, 1989), we have no data to support or refute this hypothesis. However, it does appear that differences between males and females in behavior result in females capturing more prey. Since there is a strong correlation between female foraging success and fecundity (Wise, 1993), these data indicate that differences between males and females in energetic needs for reproduction may have influenced the evolution of sex differences in morphology and behavior in spiders.

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LITERATURE CITED

- ANDERSON, R. A. AND L. J. VITT. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia*, **84**:145–157.
- ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton. 599 p.
- BOEVE, J.-L. 1994. Injection of venom into an insect prey by the free hunting spider *Cupiennius salei* (Araneae: Ctenidae). *J. Zool. Lond.*, **234**:165–175.
- AND C. MEIR. 1994. Spider venom and eco-ethological implications: a simple mathematical model. *Ecol. Modeling*, **73**:149–157.
- , L. KUHN-NENTWIG, S. KELLER AND W. NENTWIG. 1995. Quantity and quality of venom released by a spider (*Cupiennius salei*, Ctenidae). *Toxicon*, **33**:1347–1357.
- BRADY, A. R. AND K. S. MCKINLEY. 1994. Nearctic species of the wolf spider genus *Rabidosa* (Araneae: Lycosidae). *J. Arachnol.*, **22**:138–160.
- BULL, C. M. AND Y. PAMULA. 1996. Sexually dimorphic head sizes and reproductive success in the sleepy lizard *Tiliqua rugosa*. *J. Zool. Lond.*, **240**:511–521.
- CAROTHERS, J. H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.*, **124**:244–254.
- CODDINGTON, J. A., G. HORMIGA AND N. SCHARFF. 1997. Giant female or male dwarf spiders? *Nature*, **385**:687–688.

- COLLET, D. 1991. Modeling binary data. Chapman and Hall, London, U.K. 369 p.
- DARWIN, C. 1871. The descent of man and selection in relation to sex. Princeton University Press, Princeton, New Jersey. 475 p.
- DONDALE, C. D. AND J. H. REDNER. 1990. The insects and arachnids of Canada, Part 17: The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. Biosystematics Research Institute, Ottawa. 383 p.
- ELGAR, M. 1991. Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneidae). *Evolution*, **45**:444–448.
- FABER, D. B. 1984. Sexual differences in body proportions of *Zygoballus rufipes* Peckham (Araneae: Salticidae): an effect of cheliceral and leg allometry. *J. Arachnol.*, **11**:385–391.
- FAIRBAIRN, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.*, **28**:659–687.
- FOELIX, R. F. 1996. Biology of spiders, 2nd ed. Oxford University Press, Oxford U.K. 330 p.
- GIVENS, R. P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). *Ecology*, **59**:309–321.
- GOTELLI, N. J. 1995. A primer of ecology. Sunderland: Sinauer Associates, Inc., Sunderland, Mass. 206 p.
- HAGSTRUM, D. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and field. *Ann. Entomol. Soc. Am.*, **63**:1297–1304.
- HALLANDER, H. 1967. Range and movements of the wolf spiders *Pardosa chelata* (O.F. Muller) and *P. pullata* (Clerck). *Oikos*, **18**:360–364.
- HARDMAN, J. M. AND A. L. TURNBULL. 1974. The interaction of spatial heterogeneity, predator competition and the functional response to prey density in a laboratory system of wolf spiders (Araneae: Lycosidae) and fruit flies (Diptera: Drosophilidae). *J. Anim. Ecol.*, **43**:155–172.
- HAYNES, D. L. AND P. SISOJEVIC. 1966. Predatory behavior of *Philodromus rufus* Walckenaer (Araneae: Thomisidae). *Canad. Ent.*, **98**:113–133.
- HEAD, G. 1995. Selection on fecundity and variation in degree of sexual size dimorphism among spider species (Class: Araneae). *Evolution*, **49**:776–781.
- HEBBETS, E. A. AND G. W. UETZ. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.*, **47**:280–286.
- HEDRICK, A. V. AND E. J. TEMELES. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. *TREE*, **4**:136–138.
- HERREL, A., L. SPITHOVEN, R. VAN DAMME AND F. DEVREE. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.*, **13**:289–297.
- HORMIGA, G., N. SCHARFF AND J. CODDINGTON. 2000. The phylogenetic basis of sexual size dimorphism in Orb-Weaving Spiders (Araneae: Orbiculariae). *Systematic Biology*, **49**:435–462.
- JAKOB, E. M., S. D. MARSHALL AND G. W. UETZ. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**:61–67.
- JACKSON, R. R. 1982. The biology of ant-like jumping spiders; intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). *Zool. J. Linn. Soc.*, **76**:293–319.
- . 1986. The biology of ant-like jumping spiders (Araneae, Salticidae): prey and predatory behavior of *Myrmarachne* with particular attention to *M. Lupata* from Queensland. *Zool. J. Linn. Soc.*, **88**:179–190.
- JULIANO, S. A. 1993. Nonlinear curve fitting: predation and functional response curves, p. 159–182. In: S. M. Scheiner and J. Gurevitch (eds.). Design and analysis of ecological experiments. Chapman and Hall, New York.
- KASTON, B. J. 1981. Spiders of Connecticut. State Geological and Natural History Survey of Connecticut Bulletin 70 Revised Edition. Hartford, Conn. 1020 p.
- MARSHALL, S. D. AND J. L. GITTLEMAN. 1994. Clutch size in spiders: is more better? *Funct. Ecol.*, **8**:118–124.
- MORING, J. B. AND K. W. STEWART. 1992. The influence of sex and egg-case presence on predatory

- behavior of the wolf spider *Pardosa valens* Barnes (Araneae: Lycosidae). *The Southwest Naturalist*, **37**:132–137.
- PERRET, B. A. 1977. Venom regeneration in tarantula spider-I. Analysis of venom produced at different time intervals. *Comp. Biochem. Physiol.*, **56A**:607–613.
- PERRY, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Can. J. Zool.*, **74**:1238–1245.
- POLLARD, S. D. 1990. The feeding strategy of a crab spider, *Diaea* sp. indet. (Araneae: Thomisidae): post capture decision rules. *J. Zool. Lond.*, **222**:601–615.
- . 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). *J. Zool. Lond.*, **234**:203–208.
- PREEST, M. R. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *J. Herpetol.*, **28**:292–298.
- PRENTER, J., W. I. MONTGOMERY AND R. W. ELWOOD. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *J. Zool. Lond.*, **243**:341–349.
- , R. W. ELWOOD AND W. I. MONTGOMERY. 1998. No association between sexual size dimorphism and life histories in spiders. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, **265**:57–62.
- , ——— AND ———. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution*, **53**:1987–1994.
- REYNOLDS, J. D. AND P. H. HARVEY. 1994. Sexual selection and the evolution of sex differences, p. 53–70. *In*: R. V. Short and E. Balaban (eds.). *The differences between the sexes*. Cambridge University Press, Cambridge, U.K.
- RIECHERT, S. E. AND J. M. HARP. 1987. Nutritional ecology of spiders, p. 645–672. *In*: F. Slansky and J. G. Rodriguez (eds.). *Nutritional ecology of insects, mites, spiders, and related invertebrates*. John Wiley and Sons, New York.
- ROVNER, J. S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Z. Tierpsychol.*, **25**:232–242.
- . 1980. Morphological and ethological adaptations for prey capture in wolf spiders (Araneae: Lycosidae). *J. Arachnol.*, **8**:201–215.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.*, **2**:369–404.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, **68**:113–151.
- . 1972. Sexual selection and dimorphism in birds, p. 180–230. *In*: B. Campbell (ed.). *Sexual selection and the descent of man 1871–1971*. Aldine Publishing Co., Chicago.
- SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.*, **64**:419–461.
- . 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am. Nat.*, **138**:103–122.
- . 1993. Sexual dimorphism in snakes, p. 49–86. *In*: R. A. Seigel and J. T. Collins (eds.). *Snakes: ecology and behavior*. McGraw-Hill, Inc. New York.
- , P. S. HARLOW, W. R. BRANCH AND J. K. WEBB. 1996a. Life on the lowest branch: sexual dimorphism, diet, and reproductive biology of an african twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia*, **1996**:290–299.
- , W. R. BRANCH, P. S. HARLOW AND J. K. WEBB. 1996b. Sexual dimorphism, reproductive biology, and food habits of two species of African filesnakes (*Mehelya*, Colubridae). *J. Zool., Lond.*, **240**:327–340.
- TEMELES, E. J. AND W. M. ROBERTS. 1993. Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. *Oecologia*, **94**:87–94.
- VAUDRY, R., M. RAYMOND AND J. F. ROBITAILLE. 1990. The capture of voles and shrews by male and female *Mustela erminea* in captivity. *Holarctic Ecology*, **13**:265–268.
- VOLLRATH, F. 1998. Dwarf males. *TREE*, **13**:159–163.
- AND G. A. PARKER. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature*, **360**:156–159.
- AND ———. 1997. Giant females or dwarf males? a reply to Coddington *et al.* *Nature*, **385**:688.
- WISE, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, New York. 328 p.