

# Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles

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**Abstract:** Sexual dimorphism in animals is thought to be a result of differences between the sexes in the relationship between reproductive success and a trait, or a result of intersexual niche divergence. Intersexual niche divergence occurs as a result of competition between the sexes and is generally inferred from sexual dimorphism in morphological features associated with feeding. However, differences between the sexes in trophic morphology can be a result of either intersexual niche divergence or differences in the relationship between foraging success and reproduction between the sexes. In this study we examined sex differences in the trophic morphology of six wolf spider species and in the feeding behavior of two of these species. Females were larger than males in almost all characteristics even after differences in body size were accounted for, and killed and consumed more prey. We found little evidence of intersexual niche divergence based on differences in the relative prey sizes preferred by males and females of two species. Our data suggest that differences in the reproductive roles of males and females have resulted in foraging success being more important for female fitness than for male fitness and that differences in reproductive roles can result in sexual dimorphism.

**Résumé :** Le dimorphisme sexuel chez les animaux est généralement reconnu comme étant le résultat de différences entre les sexes dans la relation entre le succès à la reproduction et une caractéristique ou un résultat de la divergence de niche entre les sexes. La divergence de niche chez les deux sexes est une conséquence de la compétition entre mâles et femelles et se reconnaît généralement au dimorphisme sexuel des structures morphologiques associées à l'alimentation. Cependant, les différences de morphologie trophique chez les mâles et les femelles peuvent résulter de la divergence intersexuelle de niche, mais aussi de dissemblances dans la relation entre le succès de la quête de nourriture et la reproduction chez les mâles et les femelles. Au cours de cette étude, nous avons examiné les distinctions sexuelles dans la morphologie trophique chez six espèces de lycoses et examiné la disparité entre le comportement alimentaire des mâles et celui des femelles chez deux espèces. Les femelles se sont avérées être plus grandes dans toutes leurs caractéristiques, même après correction pour tenir compte de la taille du corps, et elles ont tué et consommé plus de proies que les mâles. Nous avons trouvé peu de preuves de divergence sexuelle de niche d'après les tailles relatives des proies préférées par les mâles et les femelles des deux espèces. Nos résultats indiquent que les rôles reproducteurs différents des mâles et des femelles font en sorte que le succès de la quête de nourriture a plus d'importance pour le fitness des femelles que pour celui des mâles et que les différences entre le rôle reproducteur des mâles et celui des femelles peuvent donner naissance au dimorphisme sexuel.

[Traduit par la Rédaction]

## Introduction

Sexual dimorphism has long fascinated evolutionary biologists, so numerous hypotheses have been proposed to explain

the differences between males and females (e.g., Darwin 1871; Hedrick and Temeles 1989; Shine 1989; Andersson 1994; Reynolds and Harvey 1994; Fairbairn 1997). Generally, these can be broken down into two categories that relate sexual dimorphism to either differences between the sexes in the relationship between a particular trait and fitness (sexual selection or differences in reproductive roles) or intersexual niche divergence, which proposes that sexual dimorphism has evolved to reduce intersexual competition (Shine 1989; Fairbairn 1997).

The primary evidence supporting the intersexual niche divergence hypothesis comes from sex differences in feeding ecology and morphological features associated with feeding (e.g., Selander 1966; Carothers 1984; Shine 1989, 1991, 1993; Vaudry et al. 1990; Shine et al. 1996a, 1996b). However, sexual dimorphism in trophic characteristics may also result from differences in reproductive roles and (or) sexual selec-

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tion (Anderson and Vitt 1990; Temeles and Roberts 1993; Perry 1996; Herrell et al. 1999; Walker and Rypstra 2001). For instance, in some species of lizard, sexual dimorphism in head size simultaneously confers an advantage in intrasexual interactions between males and allows resource partitioning between the sexes (Anderson and Vitt 1990; Preest 1994; Bull and Pamula 1996). In addition, differences between the sexes in both feeding behavior and trophic morphology may also be due to differences between males and females in the relationship between foraging success and reproduction, hereinafter referred to as the hypothesis of differences in reproductive roles (Schoener 1971; Givens 1978; Shine 1989; Walker and Rypstra 2001). For instance, females' energy needs for reproduction may be much higher than males', resulting in females consuming more prey than males (Givens 1978; Moring and Stewart 1992; Walker and Rypstra 2001). In addition, differences in trophic characteristics between males and females may also reflect selective pressures that result from differences between the sexes in their respective reproductive roles. For instance, in the wolf spider *Rabidosa rabida* (Walckenaer) (Araneae: Lycosidae), females capture and consume more prey than males and have larger chelicerae and venom glands, presumably because foraging success impacts female fitness much more than male fitness (Walker and Rypstra 2001).

The extreme sexual size dimorphism found in some species of spider has made them a classic example of this phenomenon (e.g., Darwin 1871; Elgar 1991; Vollrath and Parker 1992, 1997; Head 1995; Coddington et al. 1997; Prenter et al. 1997, 1998, 1999; Vollrath 1998; Hormiga et al. 2000). Females are usually the larger sex and as adults are generally less active than males (Vollrath and Parker 1992; Foelix 1996). In spiders, female-biased sexual size dimorphism has generally been attributed to selection for fecundity (Head 1995; Prenter et al. 1999; Hormiga et al. 2000). The hypotheses of intersexual niche divergence and differences in reproductive roles have received little attention in spiders even though there are behavioral data which suggest that these two hypotheses may be important. In many species, males and females differ greatly in their foraging behavior (Haynes and Sisojevic 1966; Hardman and Turnbull 1974; Givens 1978; Moring and Stewart 1992; Foelix 1996; Walker and Rypstra 2001). For example, adult males of many web-building species do not build webs and generally do not feed after maturity, while females continue to forage (Foelix 1996). In addition, existing data on the functional response and feeding behavior of non-web-building spiders indicate that females are more voracious predators than males (Haynes and Sisojevic 1966; Hardman and Turnbull 1974; Givens 1978; Moring and Stewart 1992; Walker and Rypstra 2001). In this study we sought to examine differences in foraging behavior and trophic morphology to determine if intersexual niche divergence or differences in reproductive roles may have influenced the evolution of sex differences in wolf spiders.

Wolf spiders are an ideal system for examining sexual dimorphism in body size, trophic morphology, and feeding behavior because males and females must physically overwhelm prey (Walker and Rypstra 2001). Thus, measuring differences in foraging behavior between males and females is not complicated by the presence of a web in females and its absence in males. In addition, several morphological fea-

tures of wolf spiders are correlated with prey capture (Rovner 1980; Walker and Rypstra 2001). Rovner (1980) found that in *R. rabida*, leg morphology (scopular hairs), chelicerae, and venom glands were important in prey capture. In addition, we have found significant differences between the sexes in the size of the chelicerae and venom glands in *R. rabida*, even after differences between males and females in body size and in the number of prey killed were accounted for (Walker and Rypstra 2001). While we have examined trophic morphology and functional response in one species (Walker and Rypstra 2001), there are no data on the extent to which sexual dimorphism in trophic morphology occurs across species or on whether there are sex differences in some aspect of prey preference which would suggest that intersexual niche divergence may have played a role in the evolution of sexual dimorphism in trophic characteristics. In this study we examined the extent of sexual dimorphism in trophic characteristics in six species of wolf spider and differences in functional response, partial prey consumption, and prey-size preference in two of these species to determine if there are sex differences in trophic morphology related to sex differences in foraging ecology. Based on the relative importance of energy in reproduction, we predicted that females would have a larger trophic apparatus (i.e., chelicerae and fangs) and would be much more voracious predators than males (i.e., consume more and larger prey than males).

## Materials and methods

### Study species

Males and female wolf spiders of six different species, *R. rabida*, *Rabidosa punctulata* (Hentz), *Schizocosa ocreata* (Hentz), *Schizocosa royneri* (Uetz and Dondale), *Pardosa milvina* (Hentz), and *Hogna helluo* (Walckenaer), were collected from Butler, Hamilton, and Clermont counties, Ohio, in 1998, preserved in 70% ethanol, and used in morphological analyses (see Table 1 for numbers collected and locality information). Our choice of species provides rather broad taxonomic coverage, since two different lycosid subfamilies and four different genera were sampled. *Schizocosa ocreata* were collected from two different localities, one in northeast Cincinnati (Hamilton County) and the other near Milford, Ohio (Clermont County), at the Cincinnati Nature Center. These two sites are separated by approximately 20 km, with numerous roadways and the Little Miami River between the two sites. This alone suggests that there is little if any immigration between the populations. In addition, a morphometric analysis indicated significant differences between the populations in the length of legs III and IV and the length and width of the sternum (Walker 2001). Thus, *S. ocreata* collected from the Cincinnati Nature Center were labeled "C" and those collected from the Hazelwood site were labeled "H", and they were treated separately in all analyses. These particular species were chosen because they represent a range of sexual dimorphism and body size in wolf spiders and we were able to collect them in sufficient numbers for morphological analysis.

*Rabidosa rabida* and *R. punctulata* both occur high in vegetation in grass or old fields and are quite agile (Brady and McKinley 1994). Although the two species occur in the same habitat and are morphologically similar, the adults are

**Table 1.** Names, collection localities, and numbers of specimens examined for morphometric analysis of trophic characteristics of six species of wolf spider.

	Collection locality	No. of males	No. of females
<i>Hogna helluo</i>	Butler Co., Ohio	30*	31*
<i>Pardosa milvina</i>	Butler Co., Ohio	30	30
<i>Rabidosia punctulata</i>	Butler Co., Ohio	30	30
<i>Rabidosia rabida</i>	Butler Co., Ohio	25	34
<i>Schizocosa ocreata</i> (C)	Clermont Co., Ohio	14	15
<i>Schizocosa ocreata</i> (H)	Hamilton Co., Ohio	15	13
<i>Schizocosa rovneri</i>	Boone Co., Ky.	13	30

\*In multivariate analyses or univariate analyses of length or width of the chelicerae, only 29 males and 30 females were used because of missing data for this species. For *S. ocreata*, "C" and "H" indicate that they were collected at the Cincinnati Nature Center and the Hazelwood site, respectively.

mature at different times of the year. Adult *R. rabida* are present in the late spring and early summer, whereas *R. punctulata* mature and mate in the fall (Eason and Whitcomb 1965). Both *S. ocreata* and *S. rovneri* occur in forested areas, but *S. ocreata* prefers upland habitats, whereas *S. rovneri* prefers bottomland forest and floodplains (Uetz and Denterlein 1979). Male *S. ocreata* are more active than the females (Cady 1984) and have lower patch-residence times (Persons 1999). In addition, hunger and different sensory modes affect patch-residence time differently in males and females (Persons 1999).

*Hogna helluo* and *P. milvina* were used in both the morphological analysis and behavioral tests. These two species were chosen because they represent two ends of a continuum in terms of body size, activity, and foraging behavior, but occur in the same habitats (Dondale and Redner 1990; Marshall and Rypstra 1999; Walker et al. 1999b; Marshall et al. 2000). Both species are widely distributed across the eastern half of the United States and are common in riparian areas and disturbed habitats (Gibson 1947; Uetz 1976; Dondale and Redner 1990; Marshall and Rypstra 1999). *Hogna helluo* is the larger of the two species and females of this species are known to dig burrows (Dondale and Redner 1990; Walker et al. 1999a). *Pardosa milvina* is the smaller of the pair and is much more active than *H. helluo* and does not construct a retreat (Dondale and Redner 1990; Walker et al. 1999b). Both species are common in agroecosystems in this region of Ohio and survive well under laboratory conditions (Marshall and Rypstra 1999).

### Morphometric analysis

Morphological measurements were made using a dissecting microscope with an attached ocular micrometer accurate to the nearest 0.05 mm (see Walker and Rypstra 2001). We used carapace width as an indicator of body size. While different characteristics may result in different estimates of size (see Prenter et al. 1994), we chose to use carapace width as an estimator of spider size because, like the trophic characteristics we are interested in, it is fixed after the adult molt (Foelix 1996) and does not vary with nutritional state (as total length does) (Anderson 1974). In addition, it has been proposed as the best linear estimate of spider size and is used throughout the literature as an indicator of spider size (e.g., Hagstrum 1971; Marshall and Gittleman 1994; Jakob et al. 1996). The trophic characteristics we measured were

the length and width of the large basal segment of the chelicera (hereinafter referred to as the paturon) and the width of the distal segment, the fang, where it attached to the paturon. While it is quite clear that other morphological features are important in prey capture (e.g., leg spination and scopular hairs; Rovner 1980), these characters were not chosen because separating the different selective pressures (sexual selection and natural selection) on leg morphology would be difficult, since in many species the legs are used in the courtship display (Hebets and Uetz 2000). Prior to analysis all variables were natural log transformed to improve normality and homogeneity of variance.

We examined the degree of sexual dimorphism in a particular characteristic using a two-way ANOVA with sex, species, and their interaction. We tested whether individual species were sexually dimorphic in a particular characteristic by constructing contrast statements that compared males with females within a species (SAS Institute Inc. 1989; Neter et al. 1990). We also estimated the degree of sexual dimorphism in each characteristic for individual species as a linear combination of parameters from the ANOVA, using the ESTIMATE statement of the GLM procedure of SAS version 6.12 (SAS Institute Inc. 1989; Neter et al. 1990). These estimates of the degree of sexual size dimorphism were simply the difference between the average log-transformed size of males and females of a particular species. We used a multivariate analysis of covariance (ANCOVA) to examine differences in trophic characteristics independently of body size (carapace width). We examined all possible interactions and in the final analysis only significant interaction terms ( $P < 0.05$ ) were retained. Significant differences in trophic morphology between the sexes within species were then determined by constructing contrast statements for each species (SAS Institute Inc. 1989; Rencher 1995). Because there was a large number of hypothesis tests for the degree of sexual size dimorphism, we applied a Bonferroni correction to adjust the  $\alpha$  level to maintain an overall type I error rate of 0.05. Thus the comparisonwise  $\alpha$  level was 0.0010.

### Functional response and relative prey size

Male and female *H. helluo* were obtained from animals bred in the laboratory that were collected from Miami University's Ecology Research Center in Butler County, Ohio. Adult male and female *P. milvina* were collected from Miami University's Ecology Research Center. In the laboratory,



spiders were held in an environmental chamber on a 14 h light : 10 h dark cycle at approximately 25°C and 70% RH. Spiders were fed a mixed diet of crickets (*Acheta domesticus*) and vestigial-winged fruit flies (*Drosophila melanogaster*) twice weekly prior to the beginning of the experiment. *Pardosa milvina* were maintained in round plastic cups, 5 cm in diameter at the base, 7 cm in diameter at the top, and 3.5 cm deep, containing 1–1.5 cm of moist peat moss substrate, and *H. helluo* were maintained in plastic cups, 6.5 cm in diameter at the base, 9 cm in diameter at the top, and 5 cm deep, containing 1–3 cm of moist peat moss substrate (see Walker et al. 1999a, 1999b). Prior to any experiments, animals were fed to satiation and then starved for 1 week to standardize hunger level.

We determined the functional response of these species by first randomly assigning male and female spiders to a prey density of 1, 2, 4, or 8 items ( $N = 5$  per prey density for *H. helluo* and  $N = 10$  per prey density for *P. milvina*). Prey were 7- to 15-mg crickets (*Acheta domesticus*) for *P. milvina* and 50- to 100-mg crickets for *H. helluo*. We placed *H. helluo* and *P. milvina* in larger round plastic containers (9 cm diameter at the base, 15 cm diameter at the top, 15 cm deep, with 2–4 cm peat moss substrate for *H. helluo*; 6.5 cm diameter at the base, 9 cm diameter at the top, 5 cm deep, with 1–2 cm peat moss substrate for *P. milvina*) 24 h prior to the experiment. Prey sizes were selected to be 20–40% of the body mass of the spiders. After 24 h we removed the spider and searched the container. We counted the prey that were completely consumed (remains could not be found), the prey killed (dead in the container), and the prey still alive.

The type of functional response was determined by examining the initial portion of the proportion killed versus the prey-density curve (Juliano 1993). If the proportion of prey killed varies with prey density in a linear fashion, then a type II functional response should have a slope significantly less than zero (negative) and a type III functional response should have a slope significantly greater than zero; if the slope is not significantly different from zero this indicates a type I response (Trexler et al. 1988). If a quadratic term is included, the same interpretation can be used as long as the coefficient for the quadratic term is less than the coefficient for the linear term. Logistic regression of the proportion killed (number killed / number presented) versus the number of prey was used to determine the type of functional response (Trexler et al. 1988; Juliano 1993). The proportion of prey partially consumed (number killed and not eaten / number eaten) was also examined using logistic regression to determine if there were differences between males and females and how the degree of partial prey consumption related to prey density. Differences between males and females in the proportion of partially consumed prey (number not completely consumed / number killed), proportion consumed, and proportion killed were determined using indicator variables included in the logistic regression model (Collett 1991).

The functional-response parameters (handling time per prey item and attack constant or instantaneous search rate) were estimated from the random predator equation, since prey densities were not held constant (i.e., prey were not added after consumption; Rodgers 1972; Juliano and Williams 1987; Juliano 1993). The random predator equation is

$$[1] \quad N_e = N_0[1 - e^{a(T_h N_e - T)}]$$

where  $N_e$  is the number of prey consumed,  $N_0$  is the initial prey density,  $a$  is the attack constant (this relates the rate of encountering prey to prey density),  $T$  is total time available, and  $T_h$  is handling time per prey item. Depending on the type of functional response being modeled,  $a$  can take various forms (Juliano 1993). For the type II functional response,  $a$  is a constant, while for a type III response,  $a$  is a function of prey density (Juliano 1993). The functional-response curves were only estimated for the total number of prey killed. We estimated  $T_h$  and  $a$  using Newton's method for finding the root of an implicit equation along with nonlinear least squares regression (for details see Juliano and Williams 1987; Juliano 1993). These parameters were estimated separately for males and females of each species.

To examine relative prey-size preferences (ratio of prey mass to spider mass) of males and females of both species, we first weighed individual spiders and individual crickets to the nearest 0.01 mg. Within a particular sex/species combination (i.e., male *H. helluo*), prey were selected to span ratios of prey mass to spider mass from 0.2 to approximately 2. Within the prey-size range for a certain sex/species combination, prey were randomly assigned to spiders. The presence or absence of prey was then noted after 6 h for *P. milvina* ( $N = 40$  for males and  $N = 39$  for females) and 3 h for *H. helluo* ( $N = 36$  for males and  $N = 62$  for females). These times were chosen on the basis of preliminary results because they result in at least 50% of the prey being consumed by both species. We used logistic regression to determine the relationship between killing a single prey item and relative prey size and sex for each species (Collett 1991).

## Results

### Morphometric analysis

Spider carapace widths ranged from 2 to 7 mm (Table 2), with *H. helluo* the largest of the species examined and *P. milvina* the smallest. Females were larger than males in all characteristics measured (Table 2). Trophic characteristics were generally more sexually dimorphic than carapace width in most species (Table 3). Also, species that were not significantly dimorphic in carapace width tended to be significantly dimorphic in trophic characteristics (Table 3). All trophic characteristics measured were positively correlated with body size and all scaled similarly with body size across species and sexes (Table 4). After accounting for differences in carapace width using ANCOVA, there was still significant female-biased sexual dimorphism in trophic characteristics in all species studied (Tables 4 and 5). While certain trophic characteristics were not significantly dimorphic (e.g., paturon length in *S. ocreata* (H)), the results of both multivariate univariate analyses support the contention that both males and females exhibit a significant degree of female-biased sexual dimorphism in trophic characters (Table 5).

### Functional response, partial prey consumption, and prey-size preferences

Both *H. helluo* and *P. milvina* exhibited a type II functional response, with a difference between males and females in the number of prey killed (Table 6, Figs. 1 and 2). In both

**Table 2.** Body sizes (carapace width) and trophic characteristics (paturon length and width and fang width) (mean  $\pm$  1 SE) of six species of wolf spider.

	Sex	Carapace width (mm)	Paturon length (mm)	Paturon width (mm)	Fang width (mm)
<i>H. helluo</i>	Male	5.3 $\pm$ 0.1	2.8 $\pm$ 0.05	1.12 $\pm$ 0.1	0.51 $\pm$ 0.01
	Female	6.8 $\pm$ 0.07	4.3 $\pm$ 0.05	2.06 $\pm$ 0.1	0.83 $\pm$ 0.08
<i>P. milvina</i>	Male	2.1 $\pm$ 0.03	0.94 $\pm$ 0.01	0.38 $\pm$ 0.003	0.14 $\pm$ 0.003
	Female	2.4 $\pm$ 0.02	1.2 $\pm$ 0.02	0.58 $\pm$ 0.007	0.19 $\pm$ 0.003
<i>R. punctulata</i>	Male	4.9 $\pm$ 0.04	2.6 $\pm$ 0.03	1.1 $\pm$ 0.02	0.42 $\pm$ 0.009
	Female	5.2 $\pm$ 0.05	3.2 $\pm$ 0.04	1.4 $\pm$ 0.02	0.59 $\pm$ 0.01
<i>R. rabida</i>	Male	4.9 $\pm$ 0.1	2.5 $\pm$ 0.07	1.1 $\pm$ 0.03	0.51 $\pm$ 0.01
	Female	5.8 $\pm$ 0.1	3.3 $\pm$ 0.06	1.5 $\pm$ 0.03	0.69 $\pm$ 0.01
<i>S. ocreata</i> (C)	Male	3.3 $\pm$ 0.04	1.5 $\pm$ 0.04	0.75 $\pm$ 0.02	0.26 $\pm$ 0.007
	Female	3.4 $\pm$ 0.06	1.7 $\pm$ 0.04	0.94 $\pm$ 0.03	0.32 $\pm$ 0.008
<i>S. ocreata</i> (H)	Male	3.3 $\pm$ 0.04	1.5 $\pm$ 0.03	0.71 $\pm$ 0.02	0.27 $\pm$ 0.005
	Female	3.4 $\pm$ 0.07	1.7 $\pm$ 0.03	0.92 $\pm$ 0.02	0.31 $\pm$ 0.007
<i>S. rovneri</i>	Male	3.1 $\pm$ 0.04	1.4 $\pm$ 0.04	0.67 $\pm$ 0.02	0.26 $\pm$ 0.006
	Female	3.2 $\pm$ 0.04	1.7 $\pm$ 0.04	0.89 $\pm$ 0.01	0.33 $\pm$ 0.008

**Note:** For *S. ocreata*, "C" and "H" indicate that they were collected at the Cincinnati Nature Center and the Hazelwood site, respectively.

**Table 3.** Estimated degree of sexual size dimorphism in carapace width, paturon length and width, and fang width using ANOVA.

	Carapace width	Paturon length	Paturon width	Fang width
<i>H. helluo</i>	<b>0.249 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.424 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.533 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.490 <math>\pm</math> 0.03 (&lt;0.0001)</b>
<i>P. milvina</i>	<b>0.141 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.283 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.423 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.316 <math>\pm</math> 0.03 (&lt;0.0001)</b>
<i>R. punctulata</i>	0.041 $\pm$ 0.02 (0.0330)	<b>0.182 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.225 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.346 <math>\pm</math> 0.03 (&lt;0.0001)</b>
<i>R. rabida</i>	<b>0.168 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.293 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.325 <math>\pm</math> 0.02 (&lt;0.0001)</b>	<b>0.305 <math>\pm</math> 0.03 (&lt;0.0001)</b>
<i>S. ocreata</i> (C)	0.026 $\pm$ 0.03 (0.3520)	<b>0.135 <math>\pm</math> 0.03 (&lt;0.0001)</b>	<b>0.233 <math>\pm</math> 0.03 (&lt;0.0001)</b>	<b>0.211 <math>\pm</math> 0.04 (&lt;0.0001)</b>
<i>S. ocreata</i> (H)	0.030 $\pm$ 0.03 (0.2800)	0.078 $\pm$ 0.03 (0.0238)	<b>0.262 <math>\pm</math> 0.03 (&lt;0.0001)</b>	0.115 $\pm$ 0.04 (0.0056)
<i>S. rovneri</i>	0.056 $\pm$ 0.03 (0.0234)	<b>0.160 <math>\pm</math> 0.03 (&lt;0.0001)</b>	<b>0.295 <math>\pm</math> 0.03 (&lt;0.0001)</b>	<b>0.223 <math>\pm</math> 0.04 (&lt;0.0001)</b>

**Note:** Values are presented as the estimate  $\pm$  1 SE, with the *P* value from the contrast testing for significant sexual dimorphism in parentheses. For *S. ocreata*, "C" and "H" indicate that they were collected at the Cincinnati Nature Center and the Hazelwood site, respectively. Values in boldface type are significant;  $\alpha = 0.0010$  following Bonferroni correction.

**Table 4.** Results of multivariate ANCOVA examining differences between the sexes and species in trophic characteristics and estimated slope of the relationship between them for each characteristic and carapace width, with corresponding 95% confidence intervals (CI).

(A) Multivariate ANCOVA.				
Effect	Wilks' $\lambda$	<i>F</i>	df	<i>P</i>
Log(carapace width)	0.3349	212.5	3,121	<0.0001
Species	0.2870	27.99	18,908.41	<0.0001
Sex	0.2299	358.3	3,321	<0.0001
Species $\times$ sex	0.6883	7.123	18,908.41	<0.0001
(B) Estimated slope of trophic characteristics versus carapace width.				
Character	Slope	SE	Lower 95% CI	Upper 95% CI
Log(paturon length)	0.8586	0.0484	0.7633	0.9538
Log(paturon width)	0.8131	0.0465	0.7216	0.9046
Log(fang width)	0.9202	0.0638	0.7947	1.0457

species, females killed and also consumed a higher proportion of prey than did males (Tables 6 and 7). In both species,  $T_h$  was greater for males than for females (Table 8;  $P < 0.02$ ). In both species the proportion of partially consumed prey increased with prey density (Table 9). Generally, partial prey consumption rarely occurred in *P. milvina* (14% in females and 3% in males in trials where prey were killed)

and did not differ significantly between the sexes (Fisher's exact test,  $P = 0.294$ ). However, partial prey consumption frequently occurred in female *H. helluo* but was rare in male *H. helluo* (31% in females and 6% in males in trials where prey were killed). Female *H. helluo* were much more likely to partially consume prey than were males (Fisher's exact test,  $P = 0.016$ ). Since few male spiders ( $N = 2$  for both

**Table 5.** Results of contrast statements testing for sexual dimorphism and estimates of sex differences in trophic characteristics using ANCOVA to account for differences in body size (carapace width).

	Paturon length	Paturon width	Fang width	Multivariate contrast
<i>H. helluo</i>	<b>0.211 ± 0.02 (&lt;0.0001)</b>	<b>0.332 ± 0.02 (&lt;0.0001)</b>	<b>0.261 ± 0.03 (&lt;0.0001)</b>	$F_{[3,321]} = 128, P < 0.0001$
<i>P. milvina</i>	<b>0.162 ± 0.02 (&lt;0.0001)</b>	<b>0.308 ± 0.02 (&lt;0.0001)</b>	<b>0.186 ± 0.02 (&lt;0.0001)</b>	$F_{[3,321]} = 128, P < 0.0001$
<i>R. punctulata</i>	<b>0.145 ± 0.02 (&lt;0.0001)</b>	<b>0.192 ± 0.02 (&lt;0.0001)</b>	<b>0.309 ± 0.02 (&lt;0.0001)</b>	$F_{[3,321]} = 108, P < 0.0001$
<i>R. rabida</i>	<b>0.149 ± 0.02 (&lt;0.0001)</b>	<b>0.188 ± 0.02 (&lt;0.0001)</b>	<b>0.150 ± 0.03 (&lt;0.0001)</b>	$F_{[3,321]} = 55, P < 0.0001$
<i>S. ocreata</i> (C)	<b>0.113 ± 0.02 (&lt;0.0001)</b>	<b>0.212 ± 0.02 (&lt;0.0001)</b>	<b>0.187 ± 0.03 (&lt;0.0001)</b>	$F_{[3,321]} = 39, P < 0.0001$
<i>S. ocreata</i> (H)	0.052 ± 0.02 (0.0238)	<b>0.237 ± 0.02 (&lt;0.0001)</b>	0.087 ± 0.03 (0.0074)	$F_{[3,321]} = 35, P < 0.0001$
<i>S. rovnieri</i>	<b>0.112 ± 0.002 (&lt;0.0001)</b>	<b>0.250 ± 0.02 (&lt;0.0001)</b>	<b>0.175 ± 0.03 (&lt;0.0001)</b>	$F_{[3,321]} = 29, P < 0.0001$

**Note:** Values are presented as the estimate ± 1 SE, with *P* values for comparison of males with females in parentheses. For *S. ocreata*, "C" and "H" indicate that they were collected at the Cincinnati Nature Center and the Hazelwood site, respectively. Values in boldface type are significant;  $\alpha = 0.0010$  following Bonferroni correction.

**Table 6.** Results of a logistic regression to determine the type of functional response for each species.

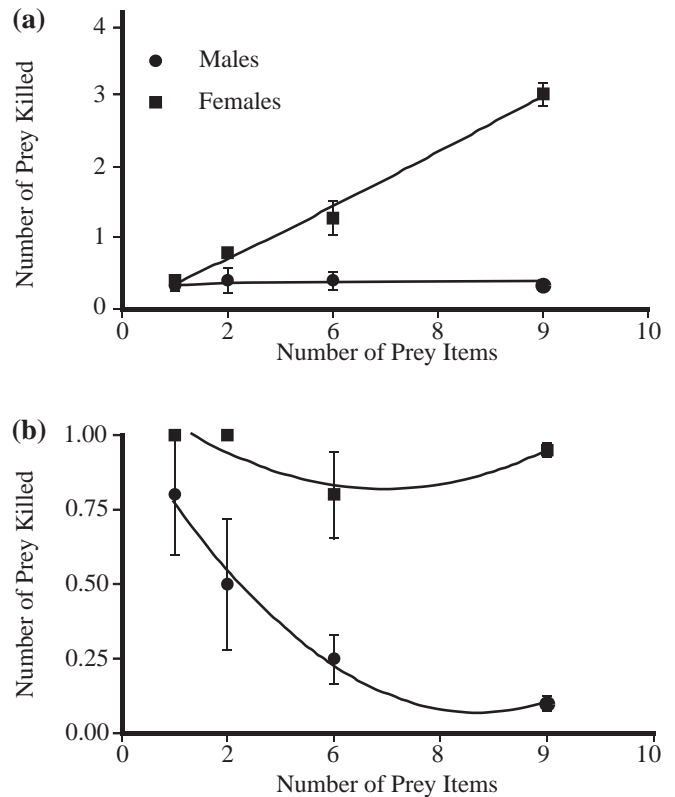
	df	Estimate	SE	$\chi^2$	<i>P</i>
<i>Hogna helluo</i>					
Intercept	1	3.09	1.35	5.2	0.0222
$N_o$	1	-1.82	0.66	7.4	0.0064
$N_o^2$	1	-0.15	0.06	5.6	0.0176
Sex	1	3.99	0.55	52.4	<0.0001
<i>Pardosa milvina</i>					
Intercept	1	0.39	0.32	1.43	0.2309
$N_o$	1	-0.37	0.05	41.4	<0.0001
Sex	1	2.01	0.31	42.1	<0.0001

**Table 7.** Results of logistic regression for each species to determine differences between males and females in the proportion of prey consumed and the type of functional response exhibited.

	df	Estimate	SE	$\chi^2$	<i>P</i>
<i>Hogna helluo</i>					
Intercept	1	3.31	1.14	8.4	0.0036
$N_o$	1	-1.94	0.55	12.3	0.0005
$N_o^2$	1	-0.16	0.05	8.9	0.0028
Sex	1	1.39	0.44	10.1	0.0014
<i>Pardosa milvina</i>					
Intercept	1	1.73	0.72	5.85	0.0156
$N_o$	1	-1.10	0.35	9.67	0.0019
$N_o^2$	1	0.07	0.03	3.73	0.0532
Sex	1	1.73	0.33	27.7	<0.0001

*H. helluo* and *P. milvina*) actually partially consumed prey items, we only examined the relationship between the proportion of partially consumed prey and prey density for females. The proportion of partially consumed prey increased with prey density in both species (Table 9).

Male and female *H. helluo* did not attack the same-sized prey (Table 10). Males were more likely to attack prey smaller than themselves and females were more likely to attack prey larger than themselves, as evidenced by the significant interaction between relative prey size and sex (Table 10). Since females were approximately 1.5 times larger than males, this would result in very little overlap in preferred prey sizes between males and females. In both male and female *P. milvina*, as relative prey size increased, the likelihood that they would be attacked decreased (Table 10). While females were more

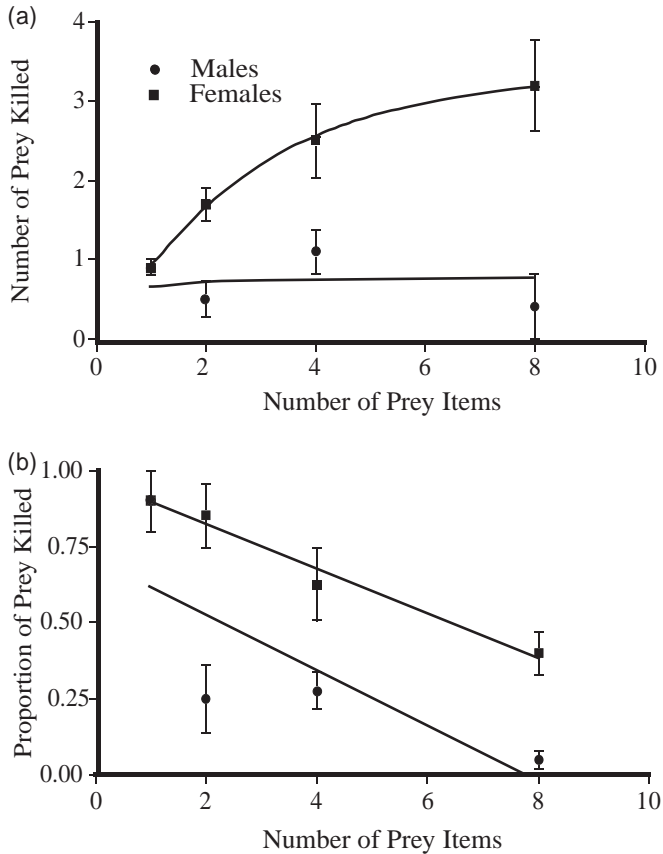
**Fig. 1.** Effect of initial prey density and sex on the number of prey killed (a) and proportion of prey killed (b) for *Hogna helluo*. The number of prey killed increased with initial prey density and females killed more prey than did males. The line represents the fit of the data to a type II functional response equation or logistic regression. Values are shown as the mean ± 1 SE.

likely to attack prey than were males, the relationship between relative prey size and the likelihood of a prey item being attacked were the same (Table 10). Thus, both male and female *P. milvina* tended to attack smaller prey than themselves, but females were more likely to attack prey than were males.

## Discussion

Female wolf spiders were generally larger than males in most characteristics. However, females almost always had

**Fig. 2.** Effect of initial prey density and sex on the number of prey killed (a) and proportion of prey killed (b) for *Pardosa milvina*. The number of prey killed increased with initial prey density and females killed more prey than did males. The line represents the fit of the data to a type II functional response equation or logistic regression. Values are shown as the mean  $\pm$  1 SE.



larger trophic characteristics than males, even after differences in body size were accounted for. In addition, our examination of feeding behavior in two species of wolf spider that differ greatly in lifestyle suggests that females have been selected to maximize their energy intake by attacking more prey, and in some cases larger prey.

In cases where sex differences in size of the chelicerae have been studied, most document that males have larger chelicerae than females and propose that this is due to intrasexual selection (Rovner 1968; Jackson 1982, 1986; Faber 1984; Pollard 1994). Interestingly, in the jumping spider *Myrmarachne lupata* (L. Koch), males have much larger chelicerae than females (approximately 5 times larger) but are less able to capture prey because of the unwieldy nature of their extraordinarily large chelicerae (Jackson 1986). In this case, males settle intrasexual contests by spreading the chelicerae and pushing up against each other, and the sex differences in the size of the chelicerae can be explained by sexual selection (Jackson 1982). However, because these sex differences also have a negative effect on prey capture, energy acquisition is probably more important for females than for males. Our data show a similar pattern in terms of energy acquisition and prey capture (females capture and consume more prey than males) but the opposite pattern in terms of the size of the chelicerae (males have smaller chelicerae than

**Table 8.** Estimates of type II functional response parameters for *H. helluo* and *P. milvina*.

	Attack constant ( $a$ )	Handling time per prey item ( $T_h$ )
<i>Hogna helluo</i>		
Males	0.287 (0.770)	24.61 (6.53)
Females	0.071 (0.042)	-1.97 (3.68)
<i>Pardosa milvina</i>		
Males	0.24 (0.818)	31.22 (10.4)
Females	0.127 (0.09)	6.30 (1.47)

**Note:** The total number of prey killed was used as the response variable in the non-linear regression. Values in parentheses show the standard error.

**Table 9.** Results of logistic regression examining differences in the proportion of prey that were partially consumed for females of both species.

	df	Estimate	SE	$\chi^2$	$P$
<i>Hogna helluo</i>					
Intercept	1	-1.77	0.65	7.44	0.0064
$N_o$	1	0.325	0.10	10.1	0.0015
<i>Pardosa milvina</i>					
Intercept	1	-3.53	0.86	16.7	<0.0001
$N_o$	1	0.374	0.13	8.67	0.0032

**Table 10.** Results of logistic regression to examine differences in relative prey size preferences between the sexes for both species.

	df	Estimate	SE	$\chi^2$	$P$
<i>Hogna helluo</i>					
Intercept	1	1.37	0.95	2.1	0.1495
Relative prey size	1	-1.35	1.47	0.84	0.3591
Sex	1	-2.99	1.18	6.11	0.0134
Interaction	1	3.74	1.82	4.23	0.0396
<i>Pardosa milvina</i> *					
Intercept	1	2.27	0.77	8.77	0.0031
Relative prey size	1	-3.15	0.89	12.38	0.0004
Sex	1	3.02	0.78	15.08	<0.0001

\*The interaction term was left out of this model because it was not significant (likelihood-ratio test,  $\chi^2_{[1]} = 0.184$ ,  $P = 0.6679$ ).

females). This pattern of differences in trophic characteristics between males and females is the opposite of what would be predicted as a consequence of sexual selection. For example, if males were fighting with their chelicerae, one would expect their chelicerae to be larger than females', not smaller (Rovner 1968; Jackson 1982; Faber 1984; Pollard 1994). This suggests that intersexual niche divergence, or differences in the reproductive roles of males and females, may be an important factor determining sex differences in trophic morphology.

The type II functional response of male and female *H. helluo* and *P. milvina* is consistent with the results of other studies of spiders (see Wise 1993). However, females kill and consume more prey than do males, indicating that females are probably maximizing energy intake. Males of both species, on the other hand, generally only captured one prey item regardless of prey density. These data indicate that males and



females differ in their energetic needs for reproduction and are consistent with the results of other studies of feeding behavior in male and female spiders (e.g., Haynes and Sisojevic 1966; Hardman and Turnbull 1974; Givens 1978; Moring and Stewart 1992; Walker and Rypstra 2001). The differences we observed are consistent with the hypothesis that differences in the reproductive roles of males and females have resulted in sexual dimorphism in trophic morphology and feeding behavior. Foraging success, and hence energy intake, is much more important for reproduction in females than in males. Foraging success does dictate the number of eggs a female can lay, and thus could strongly influence female fitness (Wise 1993). In addition, it has been suggested that males can increase their fitness more by meeting a minimum energy requirement (e.g., eating one prey item) and spending the rest of their time in pursuit of mates (Givens 1978).

We also examined the relative prey sizes that male and female *H. helluo* and *P. milvina* prefer. In male and female *P. milvina*, as relative prey size increases, the probability that they will attack prey decreases. However, there was no difference between male and female *P. milvina* in the relationship between relative prey size and the probability that they would be attacked. Therefore, male and female *P. milvina* were much more likely to attack prey smaller than themselves. While these results do not unequivocally refute the idea that there is some degree of niche separation between male and female *P. milvina*, they do seem to indicate very little, if any, differences between males and females in the size of prey that they attack. However, for male and female *H. helluo* there is a striking difference in the relationship between relative prey size and probability of attack. As relative prey size increases, the probability of attack decreases in males but increases in females. Thus, since females are larger than males and prefer prey that are larger than themselves, this would result in niche separation between males and females. In addition, Givens (1978) reported a similar difference in male and female jumping spiders (*Phidippus audax*, Araneae: Salticidae). Males of this species preferred smaller prey than did females. While these data are consistent with the niche-divergence hypothesis, they are also consistent with differences in energetic needs for reproduction. These two hypotheses may result in the same pattern of morphological differences but arrive through different mechanisms. The niche-divergence hypothesis suggests that the differences between the sexes are due to intrasexual competition, whereas sexual dimorphism resulting from differences in reproductive roles is due to the influence of food consumption on fitness in each sex (Shine 1989). Differentiating between these two hypotheses is quite difficult, since sex differences in trophic morphology, as well as niche divergence, could simultaneously confer a reproductive benefit (Anderson and Vitt 1990; Temeles and Roberts 1993; Preest 1994; Bull and Pamula 1996; Perry 1996; Herrell et al. 1999; Walker and Rypstra 2001). However, given that there is little evidence for competition in spiders (Wise 1993), it seems that intersexual niche divergence resulting from competition between the sexes is an unlikely scenario.

Partial prey consumption and capturing multiple prey items are two of the behaviors that increase the effects of invertebrate predators on pests (Lucas 1985; Samu 1993; Samu and

Biro 1993), and they may also indicate important behavioral differences between males and females. Partial prey consumption was quite easy to determine, because when prey were fully consumed, generally nothing was left in the container but a small ball of indigestible parts (see Samu and Biro 1993). The number of partially consumed prey relative to the total number killed increased with prey density in both female *P. milvina* and *H. helluo*, indicating that average percent consumption per prey item was decreasing, as was handling time per prey item. This is consistent with predictions from optimal foraging theory which suggest that average handling time per prey item should decrease as the number of available prey items increases (Johnson et al. 1975; Lucas 1985; Lucas and Grafen 1985; Samu 1993; Samu and Biro 1993). This would allow spiders to consume only the most profitable parts of the prey and move on to another prey item (Samu 1993). However, partial prey consumption was quite rare in male spiders (only 3% of trials with *P. milvina* and 6% of trials with *H. helluo*). Once again, these data are consistent with the hypothesis that females maximize energy intake and males minimize time and resources spent foraging.

Female spiders consumed more prey than males and did so in a manner that resulted in a much higher energy intake (i.e., they consumed more or larger prey, or both). In addition, morphological differences in trophic morphology suggested that females should be able to capture larger prey, and additional evidence (larger venom glands) suggests that females should be able to capture more prey (Walker and Rypstra 2001). Our data show that in terms of differences in behavior and morphology, wolf spiders fit a pattern which suggests that differences in reproductive roles which result in females requiring more energy for reproduction than males have influenced sexual dimorphism in feeding behavior and trophic morphology.

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