

Sexual dimorphism and the differential mortality model: is behaviour related to survival?

SEAN E. WALKER^{1*} and ANN L. RYPSTRA²

¹Department of Zoology, Miami University, Oxford, OH 45056, USA

²Department of Zoology, Miami University, 1601 Peck Boulevard, Hamilton, OH 45011, USA

Received 28 February 2002; accepted for publication 29 August 2002

There are numerous hypotheses to explain the evolution of sexual dimorphism in spiders. One of the most controversial is the differential mortality model (DMM) which proposes that differing rates of (adult) male and female mortality can result in a skewed operational sex ratio and lead to the evolution of small males. This hypothesis has been examined using a comparative approach which assumes that the behaviour of males and females could be used as a surrogate measure of mortality. We tested this assumption using two model species, *Hogna helluo* and *Pardosa milvina* (Araneae: Lycosidae) that differ in the degree of sexual dimorphism both in terms of body size and level of activity. Our data demonstrate that differences in male and female behaviour are not predictive of differences in mortality. Rather, as in other organisms, mortality is a complex phenomenon dependent on activity as well as size. These data call into question the methods previously used to test the DMM and suggest that understanding sexual size dimorphism (SSD) in spiders will require evaluation of historical constraints as well as how size currently influences fitness in each sex. © 2003 The Linnean Society of London. *Biological Journal of the Linnean Society*, 2003, 78, 97–103.

ADDITIONAL KEYWORDS: Araneae – sexual size dimorphism – differential mortality.

INTRODUCTION

Numerous hypotheses have been proposed to explain the evolution of sexual dimorphism (Darwin, 1871; Ghislen, 1974; Hedrick & Temeles, 1989; Shine, 1989; Andersson, 1994; Short & Balaban, 1994; Fairbairn, 1997). They fall into two broad camps, linking it either to reproductive success (e.g. Andersson, 1994; Fairbairn, 1997), or to the influence of ecological factors (Fairbairn, 1997). In species where males are the larger sex, male-biased sexual size dimorphism (SSD) is related to the reproductive advantage large males have over smaller ones (Andersson, 1994). Hypotheses favouring the ecological viewpoint propose that dimorphism is the result of a reduction in competition between the sexes (Shine, 1989; Fairbairn, 1997); while they have some support, it is difficult to determine exactly what the selective factors might be (e.g.

Anderson & Vitt, 1990; Preest, 1994; Bull & Pamula, 1996).

Dramatic differences in size between males and females of some species of spider have captured the attention of biologists since Darwin (e.g. Darwin, 1871; Elgar, 1991; Vollrath & Parker, 1992; Head, 1995; Coddington, Hormiga & Scharff, 1997; Vollrath & Parker, 1997; Vollrath, 1998; Hormiga, Scharff & Coddington, 2000). A model proposed by Vollrath & Parker (1992) has generated considerable controversy regarding the evolution of SSD in spiders (Coddington *et al.*, 1997; Prenter *et al.*, 1997, 1998, 1999; Vollrath & Parker, 1997; Vollrath, 1998). Vollrath & Parker (1992) suggest that differences in adult mortality between males and females produce a female-biased operational sex ratio and the corresponding reduction in male–male competition results in optimal male size at maturity being smaller than optimal female size. As a consequence, extreme female-biased SSD is predicted when males have much higher mortality than females.

Although the differential mortality model (DMM)

*Corresponding author. Present address: Department of Biological Sciences, University of Lethbridge, Lethbridge, Alberta, T1K 3M4, Canada. E-mail: sean.walker@uleth.ca

has some logical appeal, the evidence used to support it has been questioned. Vollrath & Parker (1992) used comparative data and treated species as independent data points in support of their model. However, when phylogeny is taken into account there is little support for their hypothesis (Head, 1995; Coddington *et al.*, 1997; Prenter *et al.*, 1997, 1998, 1999; Hormiga *et al.*, 2000). For example, Vollrath & Parker (1992) showed that in the extremely sexually dimorphic species *Nephila clavipes* (Araneae: Tetragnathidae), the patterns of mortality fit their model. However, when the evolution of size is examined throughout the genus *Nephila*, female size has increased a great deal while male size has increased to a much lesser degree.

Coddington *et al.* (1997, 2000) and Hormiga *et al.* (2000) suggest that the extreme SSD in *Nephila* is the result of female gigantism rather than reduction in male size, or male dwarfism as suggested by Vollrath & Parker (1992, 1997) and Vollrath (1998). While this approach has merit, it does not address the fact that females are generally larger than males and that even with extreme changes in female size there is little change in male size. In addition, differential adult mortality can result in a female-biased operational sex ratio and a corresponding reduction in the strength of selection for large male size. Empirical studies support the proposition that such ratios result in decreased intensity of sexual selection on male traits (see Jirotkul, 1999 and references therein). DMM would thus appear to confirm sexual dimorphism, based on differences in the relationship between body size and reproductive success in females and males (i.e. size is more important for reproductive success in the former than in the latter (Andersson, 1994)). So, while extreme dimorphism may generally be a result of selection acting on female size (e.g. Head, 1995; Coddington *et al.*, 1997; Prenter *et al.*, 1997, 1998, 1999; Hormiga *et al.*, 2000) differential adult mortality may still influence the degree of sexual dimorphism through its effects on the relationship between male size and fitness (Vollrath & Parker, 1992; Vollrath, 1998).

One of the main assumptions made by Vollrath & Parker (1992), Vollrath (1998), and Prenter *et al.* (1997, 1998) is that there is a link between differences in behaviour and mortality across taxa. They hypothesized that males and females with similar life-styles (i.e. both are mobile and active) should have similar rates of adult mortality whereas males and females with different life-styles (i.e. active males and sedentary females) should have dissimilar ones. In most of the comparative analyses testing the DMM, behaviour has been used as a surrogate measure of mortality (Vollrath & Parker, 1992; Prenter *et al.*, 1997, 1998; Vollrath, 1998). The objectives of this study were to examine the validity of this assumption using two

model species, *Hogna helluo* and *Pardosa milvina*, which occur in similar habitats but differ in their patterns of activity and degree of SSD.

STUDY SPECIES

Hogna helluo and *Pardosa milvina* (hereafter *Hogna* and *Pardosa*) do not build webs to capture prey and are both wolf spiders (Lycosidae: Araneae) (Dondale & Redner, 1990). They occupy similar habitats but differ in behaviour, body size, and degree of SSD (Dondale & Redner, 1990; Marshall & Rypstra, 1999; Walker *et al.*, 1999a; Marshall, Rypstra & Walker, 2000; Walker, 2001; Walker & Rypstra, 2002). *Hogna* is the larger of the two species (female carapace width ~6.5 mm) and female *Hogna* are known to dig burrows whereas males do not (Dondale & Redner, 1990; Walker, Marshall & Rypstra, 1999b). In addition, *Hogna* is more sexually dimorphic than *Pardosa* (Walker, 2001). *Pardosa* is the smaller of the pair (female carapace width ~2 mm); neither males nor females construct a retreat and both are generally more active than *Hogna* (Dondale & Redner, 1990; Walker *et al.*, 1999a). Thus, based on Vollrath & Parker's (1992) assumptions, we would predict differences in locomotor activity and survival between male and female *Hogna* but not between male and female *Pardosa*.

MATERIAL AND METHODS

Hogna and *Pardosa* were collected from soybean fields at Miami University's Ecology Research Center in Butler Co., OH, USA in the spring and summer of 1998. To verify our observations about sexual dimorphism, we collected 21 male and 21 female *Hogna* and 28 male and 27 female *Pardosa* and measured the carapace width of each spider using dial calipers to the nearest 0.1 mm. This was used as an indicator of spider body size because it has been proposed as providing the best linear estimate and is used extensively (e.g. Hagstrum, 1971; Marshall & Gittleman, 1994; Jakob, Marshall & Uetz, 1996).

For the laboratory experiments, spiders were collected from the field as immatures and raised to adulthood in the lab. This ensured that all spiders had not mated, since this may influence activity. Spiders were held in an environmental chamber on a 14 : 10 L : D light cycle at approximately 25°C and 70% RH. They 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* were maintained in 100 mL plastic cups with 1–1.5 cm of moist peat moss substrate and *Hogna* were maintained in 150 mL plastic cups with 2–3 cm of moist peat moss substrate (see Walker

et al., 1999a,b). Prior to experiments, animals were fed to satiation and then starved for 1 week to standardize hunger level.

Locomotor activity was monitored for 30 min using a video-based data acquisition system (Walker *et al.*, 1999a; Persons *et al.*, 2001). Spiders were placed in a round container 20 cm in diameter and given 30 min to acclimate. Their activity was then monitored using a video camera (JVC high band Saticon GXS 700) and Videomex-V (Columbus Instruments, Columbus OH, USA). The latter was set to automatically monitor speed (cm/s) time spent moving (s) and total distance (cm) travelled every 3 min. Total distance travelled was calculated by summing ten 3-minute intervals over the 30 minute trial. Average speed was calculated based on the total number of speed measurements made during these intervals. Intervals in which the animal did not move were not included in the calculation. We used the maximum measured speed as an index of locomotor performance (e.g. Walker *et al.*, 1999a). This was determined by examining the speed measurement for each interval and picking the fastest. Animals that did not move during the trial were not used in the analysis of speed but were used in the analysis of total distance travelled ($N = 2$ *Pardosa* females, $N = 1$ *Hogna* female). Analysis of locomotor and morphological data was done using a two-way ANOVA with sex and species as factors. To meet assumptions of ANOVA, carapace width, average speed and maximum speed were natural log transformed and total distance travelled was square-root transformed.

We also examined differences in the survival of male and female *Hogna* and *Pardosa* in the field using enclosures. For these experiments, *Pardosa* were collected in the field as adults or subadults and maintained for approximately 2 weeks in the lab. We tried to ensure that female *Pardosa* had not mated by only using those that had not laid an egg case during this period. This was based on data showing that when egg cases are removed from females they construct a new egg case in an average of 11 days (S. E. Walker, pers. obs.; Persons, Walker & Rypstra, 2002). All *Hogna* were collected as subadults and raised to maturity in the lab (methods as above). To maintain conditions similar to those in the laboratory experiments, we fed animals to satiation 1 week prior to beginning the experiments. These were conducted in six 0.42 ha conservation tillage soybean fields (description in Marshall & Rypstra, 1999; Marshall *et al.*, 2000) at Miami University's Ecology Research Center during July and the beginning of August of 1998 (*Hogna*) and 1999 (*Pardosa*). Four 2.25 m² aluminium flashing enclosures were constructed in each field in each year; the walls were approximately 0.4 m high and coated with a light layer of Tangle Trap (The

Tanglefoot Company, Grand Rapids, MI) around the inside edge to prevent spiders from climbing out. We intentionally left weeds and soybeans inside the enclosures to provide habitat unless they were up against or hanging over the side of the enclosure. Any vegetation hanging over the side was trimmed back so that spiders could not climb up it and escape. Any invertebrate predators (e.g. other spiders and carabid beetles) or prey were left in the enclosures. To create a favourable habitat for spider prey, we added a thin layer of straw mulch (≈ 15 cm deep) and approximately 50 g of dry fruit fly media (Carolina Biological Supply, Burlington, NC) (see Marshall *et al.*, 2000). After approximately 2 weeks, we added either three *Hogna* or 16 *Pardosa* of a single sex into each enclosure, reflecting natural densities as *Pardosa* is much more abundant than *Hogna* (Marshall & Rypstra, 1999; Marshall *et al.*, 2000). In each field we had two replicates of male and female enclosures, a total of 12 for each sex. Enclosures were constructed in the first week and experiments started in the third week of July in both 1998 and 1999; they were censused following 7 days for *Pardosa* and 14 days for *Hogna*. Survival differences within species between the sexes were examined using Cochran–Mantel–Haenszel test for sets of 2×2 tables. This is appropriate since we collected binomial data in a randomized block design (plots are blocks) (Agresti, 1990; Stokes, Davis & Koch, 1995). All analyses were done using Statview 5.0 or SAS v 6.12.

RESULTS

There were significant differences between the sexes and species in carapace width, total distance travelled, average speed, and maximum speed (Table 1). Female carapace width was larger than that of males in both *Hogna* and *Pardosa* (Fig. 1, Bonferroni multiple comparison procedure, $P < 0.0001$ in both cases). However, based on the significant interaction term (Table 1), *Hogna* was more size dimorphic than *Pardosa*. *Hogna* males moved much further than *Hogna* females, whereas *Pardosa* males and females exhibited similar levels of activity (Table 2). Average and maximum speed were only significantly different between species and there were no significant effects of sex or interaction between sex and species (Tables 1, 2). *Hogna* was significantly faster than *Pardosa* (Table 2).

We also found differences in survival (Fig. 2). In both cases, these data meet the Mantel–Fleiss criterion for minimum expected cell sizes (Stokes *et al.*, 1995). Although males had lower survival rates than females there was no significant difference between male and female *Hogna* (Cochran–Mantel–Haenszel test: $\chi^2 = 0.126$, $df = 1$, $P = 0.722$) but male *Pardosa*

Table 1. Results of two-way ANOVAs examining sex and species differences in carapace width, total distance travelled, average and maximum speed

	Effect	Mean square	df	F	P
Carapace width	Sex	0.139	1,93	102.5	<0.0001
	Species	4.475	1,93	3296	<0.0001
	Sex*Species	0.028	1,93	20.544	<0.0001
Total distance travelled	Sex	1835	1,110	17.75	<0.0001
	Species	1425.7	1,110	13.79	0.0003
	Sex*Species	889.4	1,110	8.659	0.0041
Average speed	Sex	0.0002	1,107	0.013	0.9110
	Species	0.808	1,107	42.15	<0.0001
	Sex*Species	0.001	1,107	0.030	0.8626
Maximum speed	Sex	0.027	1,107	0.998	0.3200
	Species	0.678	1,107	24.73	<0.0001
	Sex*Species	0.003	1,107	0.124	0.7256

Table 2. Differences in locomotory behaviour between male and female *Hogna* and *Pardosa*. Data are presented as Means \pm 1 SE. A and B indicate significant differences between groups based on a Bonferroni multiple comparison procedure

Species and sex	Total distance travelled (cm)	Average speed (cm/s)	Maximum measured speed (cm/s)
<i>Hogna</i> female	420.3 \pm 66.5 A (N = 30)	2.74 \pm 0.15 A (N = 29)	3.45 \pm 0.21 A (N = 29)
male	1149.0 \pm 103.2 B (N = 42)	2.77 \pm 0.12 A (N = 42)	3.87 \pm 0.23 A (N = 42)
<i>Pardosa</i> female	376.6 \pm 82.4 A (N = 21)	1.902 \pm 0.18 B (N = 19)	2.61 \pm 0.32 B (N = 19)
male	431.3 \pm 77.4 A (N = 21)	1.83 \pm 0.12 B (N = 21)	2.55 \pm 0.18 B (N = 21)

had lower survival than female *Pardosa* ($\chi^2 = 35.453$, $df = 1$, $P = 0.001$).

DISCUSSION

We found that *Hogna* had greater SSD than *Pardosa*. In addition, as predicted, we found pronounced differences in activity between male and female *Hogna* but not in *Pardosa*, with male *Hogna* more active than females. We found dimorphism in survival rates, although these were not as predicted. Male *Pardosa* had higher mortality than females while male and female *Hogna* had similar mortality. These data do not support the predictions of the DMM and call into question previous assumptions when testing it.

Many authors have assumed that differences in

activity patterns are correlated with differences in mortality between the sexes across species (Vollrath & Parker, 1992; Prenter *et al.*, 1997, 1998; Vollrath, 1998). This assumption is crucial to comparative analyses that have tested the DMM since only qualitative data on the behaviour of males and female spiders (i.e. males are active and females build webs) are available for most species and there are almost no data on mortality (Vollrath & Parker, 1992; Prenter *et al.*, 1997, 1998; Vollrath, 1998). Our data suggest that it does not hold. The most effective way of examining the validity of the DMM would be to examine a number of different populations of a single species and determine whether there is a correlation between sex differences in mortality, the intensity of sexual selection on male size, and the degree of sexual dimorphism.

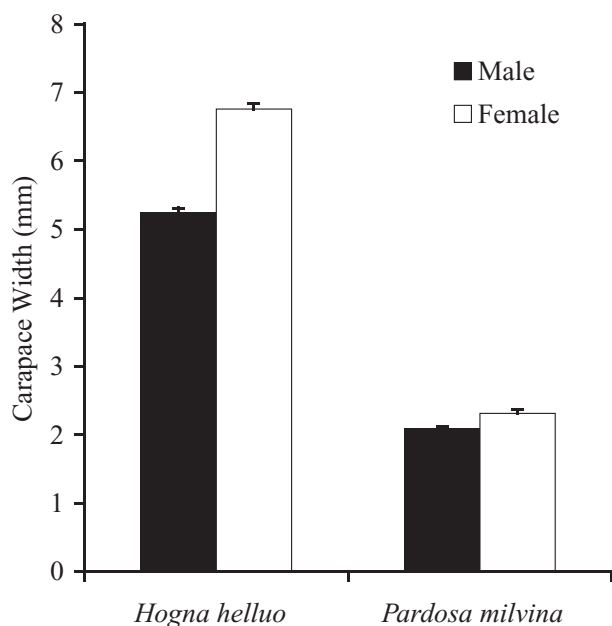


Figure 1. Sex differences in carapace width in *Hogna* and *Pardosa*. All possible pairwise comparisons between the species and sexes are significant based on a Bonferroni multiple comparison procedure. Data are shown as means \pm 1 SE.

Research has shown that an increased level of activity is correlated with an increased risk of predation (Diaz, 1993; Skelly, 1994; Anholt, Werner & Skelly, 2000; Clobert *et al.*, 2000; Eklov & Werner, 2000; Persons *et al.*, 2001; Richardson, 2001), although many of these studies are of vertebrates (in particular amphibian larvae). One might hypothesize that male *Hogna* should have fairly high predation risk and mortality. However, there is a complex relationship between predation risk, level of activity and body size (Caldwell, Thorpe & Jerve, 1980; Travis *et al.*, 1985; Scrimgeour, Culp & Wrona, 1994; Eklov & Werner, 2000; Relyea, 2001a, b; Richardson, 2001). In some cases, large size, which may make the prey too large to tackle, permits escape from a predator. Potential predators of both *Hogna* and *Pardosa* in this system include wasps, carabid beetles, and, of course, other spiders (for a discussion of predators of spiders see Wise, 1993). In many invertebrates, predator size is correlated with prey size and larger predators tend to take a wider variety of prey (Hespenheide, 1973; Enders, 1975; Nentwig & Wissel, 1986; Warren & Lawton, 1987; Reitze & Nentwig, 1991). While male *Hogna* are very active relative to female *Hogna*, they are also fairly large and thus potentially dangerous prey. Their high activity level coupled with large size may therefore result in reduced predation risk. Male *Pardosa* are very small and have a wide range of potential

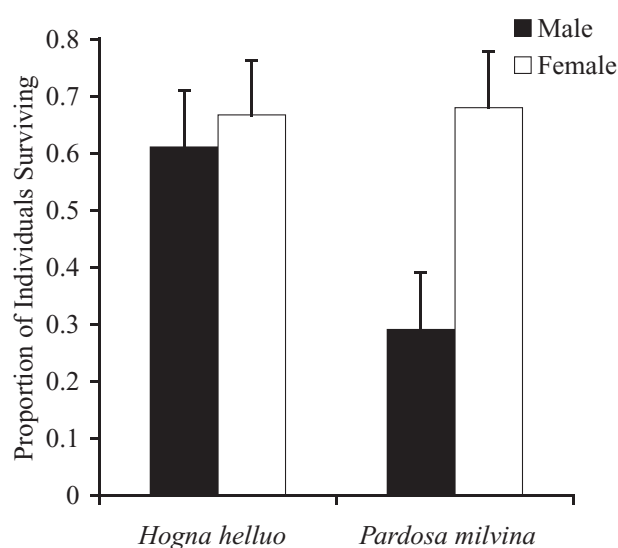


Figure 2. Proportion of individuals surviving in field enclosures of both *Hogna* and *Pardosa*. Data are shown as means \pm 1 SE.

predators, including other *Pardosa*. In addition, *Pardosa* is generally active during the day when predators such as birds are present whereas *Hogna* is generally active at night (A. L. Rypstra, S. D. Marshall, & S. E. Walker pers. observ.). Thus, mortality differences between male and female *Pardosa* may be more closely related to the number of predators than to differences in activity.

Ghislen (1974) hypothesized that highly mobile, small males would occur in systems where females are immobile and occur at low densities. This could explain the differences we observed in behaviour and dimorphism between *Hogna* and *Pardosa*. *Hogna* occurs at lower densities than *Pardosa* (Marshall & Rypstra, 1999; Marshall *et al.*, 2000); *Hogna* females are relatively sedentary compared to males and also build retreats (Walker *et al.*, 1999a,b). In addition, Legrand & Morse (2000) have proposed a similar hypothesis for a crab spider. However, since our data are for only two species, they must be interpreted with caution. Further research is required to evaluate the relationship between male size, fitness and mobility under different conditions.

While models are useful in generating hypotheses about the evolution of sexual dimorphism and body size (e.g. Wiklund & Fagerstrom, 1977; Fagerstrom & Wiklund, 1982; Vollrath & Parker, 1992; Iwasa & Haccou, 1994; Zonneveld, 1996; Crowley, 2001), they must be tested and evaluated carefully. Tests of Vollrath & Parker's (1992) model are dependent on the assumption that differences in activity reflect differences in survival when in fact they might not. The

debate about extreme sexual dimorphism in spiders has managed to produce a basic understanding of the factors that influence it. In particular, it seems clear that selection for fecundity is an important factor (Coddington *et al.*, 1997; Prenter *et al.*, 1999; Hormiga *et al.*, 2000). However, while there are data on how size influences male fitness (Buskirk, 1975; Riechert, 1978; Vollrath, 1980; Masumoto, 1994; Watson & Lighton, 1994; Elgar & Bathgate, 1996; Schneider, 1997; Schneider *et al.*, 2000) there are few studies that simultaneously examine the strength of current selective pressures for both sexes. Understanding the evolution of SSD in spiders will require an increase in our knowledge of the benefits and consequences of size for both males and females and of the heritability and genetic covariances of male and female body size.

ACKNOWLEDGEMENTS

We thank C. Weig, E. Henley and M. Brueseke for help in the field and raising spiders. A. J. Bailer, M. A. Ebbert, T. G. Gregg, S. I. Guttman, S. D. Marshall and M. H. Persons provided advice and expertise. Funding was provided by an Ohio Board of Regents Research Challenge Grant and NSF Grant DEB 9527710.

REFERENCES

- Agresti A. 1990.** *Categorical data analysis*. New York: John Wiley.
- Anderson RA, Vitt LJ. 1990.** Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* **84**: 145–157.
- Andersson M. 1994.** *Sexual selection*. Princeton, NJ: Princeton University Press.
- Anholt BR, Werner E, Skelly DK. 2000.** Effect of food and predators on the activity of four larval ranid frogs. *Ecology* **81**: 2509–3521.
- Bull CM, Pamula Y. 1996.** Sexually dimorphic head sizes and reproductive success in the sleepy lizard *Tiliqua rugosa*. *Journal of Zoology* **240**: 511–521.
- Buskirk RE. 1975.** Aggressive display and orb defense in a colonial spider, *Metabus gravidus*. *Animal Behaviour* **23**: 560–567.
- Caldwell JP, Thorpe JH, Jervey TO. 1980.** Predator-prey relationships among larval dragonflies, salamanders and frogs. *Oecologia* **46**: 285–289.
- Clobert J, Oppliger A, Sorci G, Ernande B, Swallow JG, Garland T Jr. 2000.** Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Functional Ecology* **14**: 675–684.
- Coddington JA, Hormiga G, Scharff N. 1997.** Giant female or male dwarf spiders? *Nature* **385**: 687–688.
- Crowley PH. 2000.** Sexual dimorphism with female demographic dominance: age, size, and sex ratio at maturation. *Ecology* **81**: 2592–2605.
- Darwin C. 1871.** *The descent of man and selection in relation to sex*. Princeton, NJ: Princeton University Press.
- Diaz JA. 1993.** Breeding coloration, mating opportunities, activity and survival in the lacertid lizard, *Psammodromus algirus*. *Canadian Journal of Zoology* **71**: 1104–1110.
- Dondale CD, Redner JH. 1990.** *The insects and arachnids of Canada, part 17: The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska*. Ottawa: Biosystematics Research Institute.
- Eklöv P, Werner EE. 2000.** Multiple predator effects on size-dependent behavior and mortality of two species of anuran larvae. *Oikos* **88**: 250–258.
- Elgar M. 1991.** Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneidae). *Evolution* **45**: 444–448.
- Elgar MA, Bathgate R. 1996.** Female receptivity and male mate-guarding in the jewel spider *Gasteracantha minax* Thorell (Araneidae). *Journal of Insect Behavior* **9**: 729–738.
- Enders F. 1975.** The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). *American Naturalist* **109**: 737–763.
- Fagerstrom T, Wiklund C. 1982.** Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. *Oecologia* **52**: 164–166.
- Fairbairn DJ. 1997.** Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**: 659–687.
- Ghislen MT. 1974.** *The economy of nature and the evolution of sex*. Berkeley, CA: University of California Press.
- Hagstrum D. 1971.** Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and field. *Annals of Entomological Society of America* **63**: 1297–1304.
- Head G. 1995.** Selection on fecundity and variation in degree of sexual size dimorphism among spider species (Class: Araneae). *Evolution* **49**: 776–781.
- Hedrick AV, Temeles EJ. 1989.** The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* **4**: 136–138.
- Hespenheide HA. 1973.** Ecological inferences from morphological data. *Annual Review of Ecology and Systematics* **4**: 213–229.
- Hormiga G, Scharff N, Coddington J. 2000.** The phylogenetic basis of sexual size dimorphism in orb-weaving Spiders (Araneae: Orbiculariae). *Systematic Biology* **49**: 435–462.
- Iwasa Y, Haccou P. 1994.** ESS emergence pattern of male butterflies in stochastic environments. *Evolutionary Ecology* **8**: 503–523.
- Jakob EM, Marshall SD, Uetz GW. 1996.** Estimating fitness: a comparison of body condition indices. *Oikos* **77**: 61–67.
- Jirotkul M. 1999.** Operational sex ratio influences female preference and male–male competition in guppies. *Animal Behaviour* **57**: 287–294.
- Legrand RS, Morse DH. 2000.** Factors driving extreme sex-

- ual size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society* **71**: 643–664.
- Marshall SD, Gittleman JL. 1994.** Clutch size in spiders: is more better? *Functional Ecology* **8**: 118–124.
- Marshall SD, Rypstra AL. 1999.** Patterns in the distribution of two wolf spiders. *Environmental Entomology* **28**: 1052–1059.
- Marshall SD, Rypstra AL, Walker SE. 2000.** A test for differential colonization and competitive ability in two generalist predators. *Ecology* **81**: 3341–3349.
- Masumoto T. 1994.** Male emergence timing and mating success in the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). *Ecological Research* **9**: 159–165.
- Nentwig W, Wissel C. 1986.** A comparison of prey lengths among spiders. *Oecologia* **68**: 595–600.
- Persons MH, Walker SE, Rypstra AL. 2002.** Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Behavioral Ecology* **13**: 386–392.
- Persons MH, Walker SE, Rypstra AL, Marshall SD. 2001.** Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). *Animal Behaviour* **61**: 43–51.
- Prest MR. 1994.** Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: Why do females take smaller prey than males? *Journal of Herpetology* **28**: 292–298.
- Prenter J, Elwood RW, Montgomery WI. 1998.** No association between sexual size dimorphism and life histories in spiders. *Proceedings of the Royal Society of London B* **265**: 57–62.
- Prenter J, Elwood RW, Montgomery WI. 1999.** Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* **53**: 1987–1994.
- Prenter J, Montgomery WI, Elwood RW. 1997.** Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *Journal of Zoology, London* **243**: 341–349.
- Reitze M, Nentwig W. 1991.** Comparative investigations into the feeding ecology of six *Mantodea* species. *Oecologia* **86**: 568–574.
- Relyea RA. 2001a.** Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82**: 523–540.
- Relyea RA. 2001b.** The relationship between predation risk and antipredator responses in larval anurans. *Ecology* **82**: 541–554.
- Richardson JML. 2001.** A comparative study of activity levels in larval anurans and response to the presence of different predators. *Behavioral Ecology* **12**: 51–58.
- Riechert SE. 1978.** Games spiders play: behavioral variability in territorial disputes. *Behavioral Ecology and Sociobiology* **3**: 135–162.
- Schneider JM. 1997.** Timing of maturation and the mating system of the spider, *Stegodyphus lineatus* (Eresidae): how important is body size? *Biological Journal of the Linnean Society* **60**: 517–525.
- Schneider JM, Herberstein ME, De Crespigny FC, Ramamurthy S, Elgar MA. 2000.** Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of Evolutionary Biology* **13**: 939–946.
- Scrimgeour GJ, Culp JM, Wrona FJ. 1994.** Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. *Journal of the North American Benthological Society* **13**: 368–378.
- Shine R. 1989.** Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* **64**: 419–461.
- Short RV, Balaban E. 1994.** *The differences between the sexes*. Cambridge, UK: Cambridge University Press.
- Skelly DK. 1994.** Activity level and the susceptibility of anuran larvae to predation. *Animal Behaviour* **47**: 465–468.
- Stokes ME, Davis CS, Koch GG. 1995.** *Categorical data analysis using the SAS system*. Cary, NC: SAS Institute, Inc.
- Travis JW, Keen H, Julianna J. 1985.** The role of relative body size in a predator-prey relationship between dragonfly nymphs and larval anurans. *Oikos* **45**: 59–65.
- Vollrath F. 1980.** Male body size and fitness in the web building spider, *Nephila clavipes*. *Zeitschrift für Tierpsychologie* **53**: 61–78.
- Vollrath F. 1998.** Dwarf males. *Trends in Ecology and Evolution* **13**: 159–163.
- Vollrath F, Parker GA. 1992.** Sexual dimorphism and distorted sex ratios in spiders. *Nature* **360**: 156–159.
- Vollrath F, Parker GA. 1997.** Giant females or dwarf males? A reply to Coddington et al. *Nature* **385**: 688.
- Walker SE. 2001.** The evolution of sexual dimorphism in wolf spiders (Araneae: Lycosidae). Unpublished Dissertation. Oxford, OH: Miami University.
- Walker SE, Marshall SD, Rypstra AL. 1999b.** The effect of feeding history on retreat construction in the wolf spider *Hogna helluo* (Walckenaer). *Journal of Arachnology* **27**: 689–691.
- Walker SE, Marshall SD, Rypstra AL, Taylor DH. 1999a.** The effects of feeding history on locomotor behaviour in two species of wolf spider. *Animal Behaviour* **58**: 515–520.
- Walker SE, Rypstra AL. 2002.** Sexual dimorphism in feeding behavior and trophic morphology in wolf spiders (Araneae: Lycosidae). *Canadian Journal of Zoology* **80**: 679–688.
- Warren PH, Lawton JH. 1987.** Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* **74**: 231–235.
- Watson PJ, Lighton JRB. 1994.** Sexual selection and the energetics of copulatory courtship in the Sierra Dome spider, *Linyphia litigiosa*. *Animal Behaviour* **48**: 615–626.
- Wiklund C, Fagerstrom T. 1977.** Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* **31**: 153–158.
- Wise DH. 1993.** *Spiders in ecological webs*. New York: Cambridge University Press.
- Zonneveld C. 1996.** Being big or emerging early? Polyandry and the trade-off between size and emergence in male butterflies. *American Naturalist* **147**: 946–965.