



Mate guarding, competition and variation in size in male orb-web spiders, *Metellina segmentata*: a field experiment

JOHN PRENTER*, ROBERT W. ELWOOD† & W. IAN MONTGOMERY†

*Institute of Irish Studies
and

†School of Biology and Biochemistry, Queen's University Belfast

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In the common orb-web spider *Metellina segmentata*, males are more powerfully built with longer legs, although females are heavier because of their egg load. Males guard females before attempting to mate, and there is considerable male–male competition because of the male-biased operational sex ratio. We used a field removal experiment to examine (1) seasonal changes in the average morphology of guarding males and (2) whether there is a pool of small males that is excluded from the webs of females. Morphological measures were subjected to a principal components analysis and changes in PC scores were examined for seasonal effects and the effects of previous removal of males. The size of guarding males (PC1) increased over the season, suggesting that smaller males were increasingly excluded from webs, but the condition of guarding males (PC2) decreased, indicating that energy reserves are depleted because the males gain little access to food during the reproductive season. When guarding males were removed, smaller males were able to take up residence. Our results show that large males have a clear advantage in monopolizing females. We discuss the manner in which selection acts to maintain large male size in this spider.

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Sexual size dimorphism in animals is usually attributed to gender-specific pressures of natural or sexual selection (Darwin 1871; Slatkin 1984; Arak 1988; Shine 1989; Elgar 1992; Andersson 1994). Females usually benefit from large size because this enables them to produce more eggs. If scramble competition occurs between males, the selection for large size in males is often reduced and females may be the larger sex (e.g. Vollrath & Parker 1992). If male–male contest competition occurs, however, this may provide stronger selection for large size in males than in females, resulting in males becoming the larger sex (reviewed in Andersson 1994). Thus, size dimorphism is usually mediated by the type of competition that occurs between males. In spiders, females are usually the larger sex (e.g. Prenter et al. 1999), sometimes to a considerable degree, as occurs in the genus *Nephila* (Vollrath & Parker 1992; Elgar & Fahey 1996).

Comparative studies have sought to explain this large female size in spiders as selection for greater fecundity (e.g. Head 1995; Coddington et al. 1997; Prenter et al. 1999) or for early maturation and, hence, small size in

males (e.g. Vollrath & Parker 1992; Vollrath 1998), although evidence of early maturation in males is disputed (Prenter et al. 1997, 1998; Hormiga et al. 2000). These studies, however, generally fail to note that female spiders of some species are often of a similar size or even smaller than males. An added complexity is that shape dimorphism in spiders may be more marked than size dimorphism (Prenter et al. 1995). Females have a particularly large opisthosoma because the eggs develop in this part of the body, but in many orb-web species the males have relatively long legs. In the genus *Metellina*, for example, the adult female is heavier and has a longer body, but the male has longer legs and a larger prosoma. Furthermore, if the animals are weighed after removal of the opisthosoma, the male weighs more than the female (Prenter et al. 1995). Which sex is considered to be the larger thus depends on the measure used in the analysis. It is clear that the male is more powerfully built and the female carries much larger gametes. The nature of the sexual dimorphism in this genus thus predicts the male–male competition observed in various studies (Rubenstein 1987; Hack et al. 1997; Bridge et al. 2000).

Young males of the genus *Metellina* build webs to catch food but abandon these webs in the mating season, after their final moult to adulthood, to search for females

Correspondence and present address: J. Prenter School of Biology and Biochemistry, Queen's University Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, Northern Ireland, U.K. (email: j.prenter@qub.ac.uk).

(Rubenstein 1987). They may locate receptive females by detecting a pheromone on the web (Prenter et al. 1994a), then wait by the edge of the web until a female catches a large fly (Prenter et al. 1994b). After the female has killed the fly, the male initiates his courtship, apparently taking advantage of a temporarily reduced risk of being predated or cannibalized by the female (Prenter et al. 1994c). The male, however, may have to wait for hours or even days for the arrival of a suitably large fly (Prenter et al. 1994d), and this allows time for other males to arrive. In male-male fights for 'ownership' of the web in the genus *Metellina*, the larger males have an advantage (Hack et al. 1997; Bridge et al. 2000), and smaller males are occasionally injured or killed (personal observation). These fights, and their consequences for mating opportunities, are thus likely to provide the key selective force for large male size (Prenter et al. 1995).

Only about 50% of females have males in attendance at any one time (Prenter et al. 1994d), but those without males are smaller and tend not to have mature eggs (Prenter et al. 1994a). There is thus a patchwork of females, only some of which may warrant guarding by males at any one time, but these females often occur within a few centimetres of each other, and it is likely that several females may be monitored by a single male. A male that is excluded early in the season might still find an unguarded, receptive female at a later date. Other males, however, are also likely to arrive, including previously successful males that can copulate again within 2 h (Bridge 1999), resulting in repeated exclusion of small males. Rubenstein (1987) noted that only the largest males obtain more than one mating. Thus, at any time in the reproductive season, guarding males may be expected to be larger on average than those that are searching. Furthermore, small males may become less prevalent as guards later in the season because they may be killed in fights (personal observation) or cannibalized by females (Rubenstein 1987). The average size of males found on the webs of females is thus predicted to increase as a result of competition and cannibalism (Rubenstein 1987).

This prediction, however, does not account for the depletion of energy stores during the mate-searching period, when males feed very little or not at all. Thus, the intake of food by males is markedly reduced compared with when they build their own feeding webs.

We conducted a field removal experiment during the autumn breeding season of these spiders. Our main aims were to determine whether (1) there is a pool of available males that are smaller than the males found on females' webs and (2) the average size of guarding males changes during the season. These data should help explain why males of the genus *Metellina* are more powerfully built than females. We predicted that smaller males would wander from web to web and guard when the original guarding males were experimentally removed. Searching males are difficult to locate as they wander through the gorse bush habitat, so we could gain access to this pool of excluded males only by removing guarding males to enable previously excluded males to take up residence on a female's web, where they were easily collected for examination.

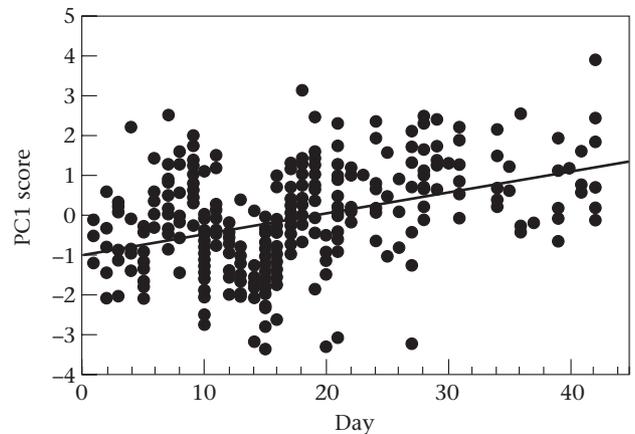


Figure 1. Seasonal changes in male size. Regression of factor scores for PC1 against day of removal.

METHODS

The study site was Lagan Meadows, a lightly grazed lowland meadow bordering the River Lagan, in the Lagan Valley Regional Park, Belfast, Northern Ireland, U.K. This was predominantly lush mixed grasses but with occasional clumps of bushes (gorse, *Ulex europaeus*, and bramble, *Rubus fruticosus*). The orb-web spider *M. segmentata* is abundant in the area in late summer and autumn. These spiders typically construct their orb webs in bushes and not grassland. We used 10 spatially isolated clumps of bushes as collection sites; each bush was separated from any neighbouring bush by at least 20 m. The sedentary habits of females and limitations on the movement of male *M. segmentata* on bushes ensured that experimental subjects were isolated from those on other bushes. If there is rapid exchange of males from various bushes, then we could not expect to gather data that would uphold our predictions (see also Prenter et al. 1994d).

Data Collection and Measurement

We examined bushes for the occurrence of webs inhabited by females that had a male in attendance. Starting on 12 September (early season group), every guarding male was removed, when first found, from the webs on three bushes. On 26 September (mid-season group), males were also removed from another four bushes and on 10 October (late-season group) from the final three bushes. Once collection started at a particular bush, it continued until 24 October (Fig. 1). The bushes were carefully surveyed twice daily, morning (0500–1000 hours) and evening (1600–2000 hours). Prenter et al. (1994d) indicated that males may arrive and leave within approximately 12–24 h and appear to be active both day and night. Males were collected in a small plastic screw-top container that we moved upwards under each male, then touched the male lightly from above, inducing it to drop into the container. The web was not damaged and the female was relatively undisturbed by this collection technique. Collected males were removed to the laboratory and the following measurements taken with a Kyowa

Table 1. Factor loadings for the PCs on the original morphological variables

	PC1	PC2
Prosoma width	0.330	0.576
Prosoma length	0.641	-0.834
Opisthosoma width	0.433	0.758
Opisthosoma length	0.506	0.206
Right leg 1 length	0.899	-0.119
Right leg 2 length	0.819	-0.176
Right leg 3 length	0.832	-0.202
Right leg 4 length	0.814	-0.181

Factor loadings above 0.6 are shown in bold. PC1 accounted for 47.5% and PC2 22.0% (total 69.5%) of the variability in the original data.

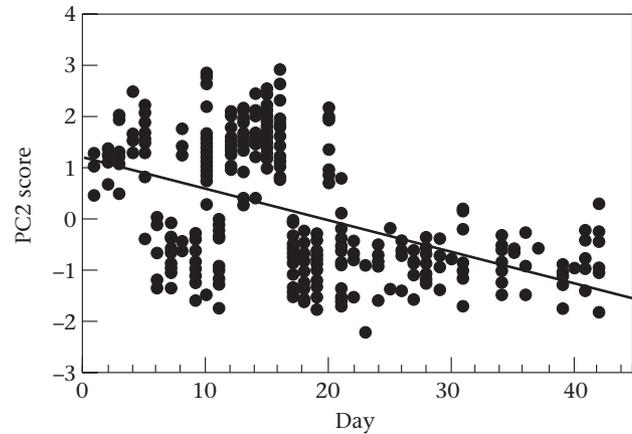
binocular microscope and graticule: length and width of the opisthosoma, length and width of the prosoma and lengths of the legs on the right side of the body.

Males found guarding on the webs of females were removed without reference to the individual female. Thus, subsequent removals are not necessarily from the webs of the same females (because females change in reproductive value). This, however, does not affect our aims to examine patterns in male size and condition of those that attain guarding positions and to investigate the effects of intrasexual selection.

Metellina segmentata has a strictly annual life cycle (Toft 1983); females mature over several weeks, but the span of male maturation is much shorter. Virtually all males had abandoned their feeding webs by the start of the collection period, and we are confident that all males had matured by the end of the first week of collection.

Statistical Analysis

Morphological data were subjected to a principal components analysis (PCA) to reduce the number of variables being examined. The PCA resulted in two PCs that we assumed to be indications of size (PC1) and body condition (PC2). We assigned size as PC1 because it loaded positively on all morphological variables, but especially on leg length and prosoma length, which are fixed for size at the final moult to adulthood. We assumed that PC2 represented a measure of body condition because it loaded especially on opisthosoma width (Table 1). The opisthosoma is not surrounded by a hardened exoskeleton and may vary in size as resources are used up. Factor scores for each of the first two PCs were used in further analyses. We used a series of one-way ANOVAs to test for between-bush effects at specific collection times; no significant effects were observed, so data within treatments were pooled in subsequent analyses (ANOVA: early bushes, weeks 1–2 of collection: PC1: $F_{2,136}=2.112$, NS; PC2: $F_{2,136}=1.743$, NS; mid bushes, weeks 3–4: PC1: $F_{3,154}=2.489$, NS; PC2: $F_{3,154}=1.630$, NS; late bushes, weeks 5–6: PC1: $F_{2,42}=0.208$, NS; PC2: $F_{2,42}=0.976$, NS). We used regressions of factor scores for principal components (PCs) against time (days of manipulation) to

**Figure 2.** Seasonal changes in body condition. Regression of factor scores for PC2 against day of removal.

examine the effects of season, and one-way independent measures ANOVAs to examine the effects of previous collection on the size of guarding males. For investigation of seasonal effects, data for the first 14 days of collection from the early-, mid- and late-season groups were compared. To examine the effects of previous collection, we used males collected from 10 to 24 October. In the early and mid sites, males were collected and removed for 4 and 2 weeks, respectively, before 10 October. These data were compared to data for the late group where there had been no previous collections.

RESULTS

Seasonal Effects

Overall male size (PC1) showed a marked increase over the breeding season (Fig. 1). We found a significantly positive relation between PC1 scores and day of collection ($R^2=0.160$; $F_{2,340}=64.535$, $P<0.0001$). In marked contrast, condition scores (PC2) for males declined over the season (Fig. 2). We observed a significant negative relation between PC2 scores and day of collection ($R^2=0.470$; $F_{2,340}=96.660$, $P<0.0001$). Thus, guarding males late in the season were larger but had poorer body condition than did those at the start. Smaller males appeared to be absent from the guarding population later in the season (Fig. 1). The size of the largest spiders (leg 1 length) did not change over the season, but the proportion of males with legs of less than 16 mm dropped from 54 to 27%, suggesting increasing exclusion of small males.

Previous Collection Effects

Males collected from sites from which guarding males had previously been removed were smaller (according to PC1 scores) than those males collected where no previous collection had occurred ($F_{2,111}=4.892$, $P<0.01$; Fig. 3). Removal of males, therefore, allowed smaller males to get to webs, replacing the larger, previously resident males. However, there was no significant effect of previous collection on PC2 score for males ($F_{2,111}=0.085$, NS).

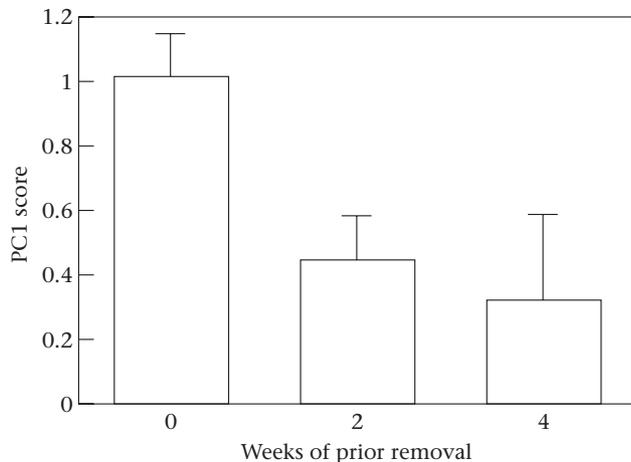


Figure 3. Effect of prior collection on male size. Results of a one-way ANOVA on factor scores for PC1 for males collected from bushes with 0, 2 or 4 weeks of previous removals. Vertical lines indicate SEs.

Body condition therefore appeared to be unaffected by previous collection.

DISCUSSION

Seasonal Effects on Size

The seasonal variation in male size (Fig. 1) supports Rubenstein's (1987) prediction that average size for males on a web should increase as an outcome of repeated intramale agonistic encounters. Thus, the population structure of guarding males in our study population changed during the mating season.

With repeated interactions over the season, it is likely that many small males are excluded or even killed. We have observed fights culminating in injury or death. Rubenstein (1987) observed females cannibalizing smaller males, and we have also observed females killing males during courtship and males giving the body of a killed rival to a female before mating (Prenter et al. 1994e). After a few fights, small males might not have been ousted entirely from the webs of females early in the season, but later, they may have lost to larger males, left the female's web and continued to wander. These factors would all produce a greater exclusion of small males from the webs of females as the season progressed. This process is supported by our results. In theory, many particularly large, late-maturing males abandoning their feeding webs late in the season could produce similar results, but in our study, almost all males had matured before the sampling period and the few that had not did so within the first week. Furthermore, the size of the largest males in the population did not increase later in the season. Variation in the timing of male maturation, therefore, does not explain the results. Thus, our results suggest selection for increased male size in *M. segmentata* as a result of mate guarding and male–male fights.

Seasonal Effects on Body Condition

Seasonal changes, i.e. shrinking of areas of the body not fixed for size at the final moult, principally the

opisthosoma, were reflected in the pattern of decreasing condition scores (PC2) over the season (Fig. 2), confirming that males were depleting their energy reserves. This result is consistent with observations that females feed exclusively on captured flies and males do not feed during courtship (Prenter et al. 1994b, c), guarding or searching. Thus, males forego opportunities to feed to secure a mating. Clearly, late in the season males are in relatively poor condition (Fig. 2), having largely exhausted reserves. This pattern is also consistent with a seasonal decrease in the weight of mate-guarding male *M. segmentata* (Prenter et al. 1994d).

The observed decline in body condition over the mating season is consistent with similar temporal relations in measures of body condition in male vertebrates (e.g. impala, *Aepyceros melampus*: Jarman 1979; red deer, *Cervus elaphus*: Clutton-Brock et al. 1982; cardinal fish, *Apogon notatus*: Okunda 2001). We predict that larger *M. segmentata* males are better able to pay the costs of fighting and maintain more favourable energy balances via lower energy expenditure associated with more sedentary guarding activities, compared with the active mate searching of smaller males forcibly excluded from webs in fights (Hack et al. 1997; Bridge et al. 2000). Larger, reproductively successful males experience reduced costs of reproduction and maintain superior body condition in elephant seals, *Mirounga angustirostris* (Clinton & Le Boeuf 1993), striped plateau lizards, *Sceloporus virgatus* (Abell 2000), and fallow deer, *Dama dama* (McElligott & Hayden 2000). Small males may be doubly disadvantaged, therefore, because reduced access to females and lower body condition will restrict the time available for reproductive activities, and lower body condition is likely to shorten life expectancy. Furthermore, increased mate-searching activity may also increase mortality in smaller males caused by predation (Vollrath & Parker 1992).

Effects of Previous Collection

We found clear evidence of male–male competition resulting in the exclusion of small males from the webs of females, and therefore from mating opportunities, by comparing males collected late in the season at sites from which previous collections had been made with those collected from control sites. Smaller males were more likely to reside on webs from which males had been removed (Fig. 3), gaining access to webs when large, reproductively successful males were absent. We conclude that larger males control access to the webs of females, and smaller males gain access only if the previous guarding males have been removed.

Rubenstein (1987) proposed size-dependent alternative mating behaviour in male *M. segmentata*. He suggested that larger males monopolize the largest females in aggregations of spiders that occur at the best feeding sites, but smaller males are left to search for solitary, smaller females in poorer-quality web sites. However, the existence of a pool of excluded males in the population, as indicated by our experimental manipulations, contradicts this suggestion.

Implications for Sexual Dimorphism

Our results indicate selection on male size via intra-sexual selection, resulting in increased fitness payoffs in terms of access to females. Comparative analyses (Head 1995; Prenter et al. 1999) and multivariate morphometric examination in *M. segmentata* (Prenter et al. 1995) suggest that females are under selection for increased fecundity, probably through selection for efficiency in predation. Thus, there appears to be selection for large size in both sexes. Sexual dimorphism, however, is not solely confined to the study of body size; there are also sexual differences in measures of shape (Prenter et al. 1995) that warrant further investigation. Furthermore, detailed examination of lifetime selection on male and female size is also warranted, because the relative effect on both sexes will determine the overall degree of sexual size dimorphism. We have not addressed male fitness directly in our study, although our findings bear on the fitness consequences of size in *M. segmentata*.

In conclusion, male *M. segmentata* are highly competitive, and larger males show increasing predominance at the webs of females as the season progresses. Small males wait and search for whatever limited opportunities arise. The extreme competition seems to be exacerbated by males attempting to avoid sexual cannibalism by waiting for the female to catch and kill a large fly (Prenter et al. 1994b, c). The delay allows rival males to locate and compete for the female. The resulting fights may lead to the exclusion or death of small males. Fighting almost certainly adds to the demands of the breeding period on both large and small males. Larger males may have a heightened ability to withstand the stress of the mating season and to maintain sufficiently good condition longer in the face of these pressures.

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References

- Abell, A. J. 2000. Costs of reproduction in male lizards, *Sceloporus virgatus*. *Oikos*, **88**, 630–640.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arak, A. 1988. Sexual dimorphism in body size: a model and a test. *Evolution*, **42**, 820–825.
- Bridge, A. P. 1999. Mating and competition in metid spiders. Ph.D. thesis, Queen's University Belfast.
- Bridge, A. P., Elwood, R. W. & Dick, J. T. A. 2000. Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina megei*. *Proceedings of the Royal Society of London, Series B*, **267**, 273–279.
- Clinton, W. L. & Le Boeuf, B. J. 1993. Sexual selection's effects on male life history and the pattern of male mortality. *Ecology*, **74**, 1884–1892.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Coddington, J. A., Hormiga, G. & Scharff, N. 1997. Giant female or dwarf male spiders? *Nature*, **385**, 687–688.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
- Elgar, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: Ecology and Evolution Among Diverse Taxa* (Ed. by M. A. Elgar & B. J. Crespi), pp. 128–155. Oxford: Oxford University Press.
- Elgar, M. A. & Fahey, B. F. 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behavioral Ecology*, **7**, 195–198.
- Hack, M. A., Thompson, J. D. & Fernandes, D. M. 1997. Fighting of males of the autumn spider, *Metellina segmentata*: the effects of relative body size, prior residency and female value on contest outcome and duration. *Ethology*, **103**, 488–498.
- Head, G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). *Evolution*, **49**, 776–781.
- Hormiga, G., Scharff, F. & Coddington, J.A. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology*, **49**, 435–462.
- Jarman, M. V. 1979. *Impala Social Behaviour: Territory, Hierarchy, Mating and the Use of Space*. Berlin: Paul Parey Verlag.
- McElligott, A.G. & Hayden, T. J. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behavioral Ecology and Sociobiology*, **48**, 203–210.
- Okunda, N. 2001. The costs of reproduction to males and females of a parental mouthbreeding cardinalfish *Apogon notatus*. *Journal of Fish Biology*, **58**, 776–787.
- Prenter, J., Elwood, R. W. & Montgomery, W. I. 1994a. Assessments and decisions in *Metellina segmentata* (Araneae: Metidae): evidence of a pheromone involved in mate guarding. *Behavioral Ecology and Sociobiology*, **35**, 39–43.
- Prenter, J., Elwood, R. W. & Colgan, S. 1994b. The influence of prey and female reproductive state on the courtship of the autumn spider *Metellina segmentata*. *Animal Behaviour*, **47**, 449–456.
- Prenter, J., Elwood, R. W. & Montgomery, W. I. 1994c. Male exploitation of female predatory behaviour: cannibalism reduction in male autumn spiders, *Metellina segmentata*. *Animal Behaviour*, **47**, 235–236.
- Prenter, J., Montgomery, W. I. & Elwood, R. W. 1994d. Patterns of mate guarding in *Metellina segmentata* (Araneae: Metidae). *Bulletin of the British Arachnological Society*, **9**, 241–245.
- Prenter, J., Elwood, R. W. & Montgomery, W. I. 1994e. Alternative mating behaviour in *Metellina segmentata* (Clerck). *Newsletter of the British Arachnological Society*, **70**, 10–11.
- Prenter, J., Montgomery, W. I. & Elwood, R. W. 1995. Multivariate morphometrics and sexual dimorphism in the orb-web spider *Metellina segmentata* (Clerck, 1757) (Araneae, Metidae). *Biological Journal of the Linnean Society*, **55**, 345–354.
- Prenter, J., Elwood, R. W. & Montgomery, W. I. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *Journal of Zoology*, **243**, 341–349.
- Prenter, J., Elwood, R. W. & Montgomery, W. I. 1998. No association between sexual size dimorphism and life histories in spiders. *Proceedings of the Royal Society of London, Series B*, **265**, 57–62.

- Prenter, J., Elwood, R. W. & Montgomery, W. I.** 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution*, **53**, 1987–1994.
- Rubenstein, D. I.** 1987. Alternative reproductive tactics in the spider *Meta segmentata*. *Behavioral Ecology and Sociobiology*, **20**, 229–237.
- Shine, R.** 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology*, **64**, 419–461.
- Slatkin, M.** 1984. Ecological causes of sexual dimorphism. *Evolution*, **38**, 622–630.
- Toft, S.** 1983. Life cycles of *Meta segmentata* (Clerck, 1757) and *Meta menzei* (Blackwall, 1869) in western Europe (Arachnida: Araneae: Tetragnathidae). *Verhandlungen Naturwissenschaftlicher Verein Hamburg*, **26**, 265–267.
- Vollrath, F.** 1998. Dwarf males. *Trends in Ecology and Evolution*, **13**, 159–163.
- Vollrath, F. & Parker, G. A.** 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature*, **360**, 156–159.