

The influence of prey size and female reproductive state on the courtship of the autumn spider, *Metellina segmentata*: a field experiment

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Abstract. Factors affecting courtship and mating behaviour in the common European orb-weaving autumn spider, *Metellina segmentata*, were examined in a field experiment. Males of this species wait on the edge of a web for the resident female to capture a prey item before entering the web to initiate courtship. Males on webs provided with large prey items (naturally occurring tipulids) exhibited more courtship behaviour and were more successful in gaining copulations than those on webs provided with small prey items. The differential success of these males was due to differences in female prey capture and retention or removal of the prey item from the web. Female reproductive state also influenced male courtship and mating behaviour. Males courted and copulated with more fecund females, perhaps as a result of these females' willingness to mate. Courtship duration and female egg load were correlated negatively and copulation duration positively with female size. Causal and functional aspects of the use of prey in this species are examined. In addition, size-assortative pairing and aspects of mate choice are discussed.

The evolution of courtship in orb-web spiders often appears to be shaped by the risk to the male of sexual cannibalism (Elgar 1991). In some species (e.g. *Nephila* spp.), the male crosses the face of the female's web to court at the hub. In others (e.g. some *Argiope* spp.), the male cuts a hole in the female's web and, within this hole, constructs a mating or nuptial thread. In species such as *Araneus diadematus*, the male attaches a nuptial thread to the side of the female's web and thus avoids going onto the web for courtship and mating. The male plucks the nuptial thread to entice the female such that mating may take place when the female assumes a typical mating posture, hanging upside-down from the thread (Robinson 1982).

In the autumn spider, *Metellina* (formerly *Meta*) *segmentata* (Clerck, 1757), courtship depends on the arrival of a prey item (Bristowe 1958; Blanke 1974). The female typically kills the prey and wraps it in silk on the web. The male then advances onto the web and forces the female away and subsequently may also wrap the prey. The male then cuts part of the web around the prey and builds a nuptial thread from which the prey is suspended, and on which mating occurs. Males may wait at the side of a female's web for several days (Rubenstein 1987),

apparently guarding the female and waiting for a chance to court. Bristowe (1958) described a high turnover of males on the webs of females. Not all prey items elicit courtship since Blanke (1974) noted that experimentally introduced *Drosophila* failed to elicit courtship but the much larger *Calliphora* invariably did.

In the present study, we examine factors that might influence the occurrence, duration and success of various courtship activities in *M. segmentata*. The effect of prey size on courtship and mating behaviour is investigated. If the involvement of prey is a male nuptial feeding strategy, males with large prey should gain more matings and have longer copulations than those with small flies (Thornhill 1976). The reproductive state of the female and the number of mature and immature eggs might also affect male mating behaviour. Males may prefer and compete for more fecund females (see Halliday 1983) resulting in size-assortative pairing (Rubenstein 1987). Female mate choice is also addressed. If females are choosy they should prefer larger males and, hence, positive correlations between male size and (1) copulation duration and (2) the frequency and/or duration of adoption of the mating position by the female, are expected. A negative correlation between male size

and courtship duration may also be predicted (but see Watson 1990; Benton 1992).

METHODS

Webs on gorse bushes near Ballycastle, Co. Antrim, Northern Ireland in 1989 containing a female with a guarding male were selected randomly and assigned to two experimental groups (large and small prey introductions, $N=60$ in each). Both a male and a female spider were required to be in contact with the web to be considered as a resident pairing. These were found commonly from early September to mid-October. To determine the role of prey in male mating behaviour, we introduced onto the web live crane-flies of two species (Tipulidae, Diptera) and of two non-overlapping size classes ($X_{\text{large}}=0.049$ g, $X_{\text{small}}=0.024$ g), previously captured at the study site and stored overnight. We tossed the flies into the hub area of a web, taking care to minimize disturbance to the web and its occupants. Only one prey item was provided on any one web. Following prey introduction, we recorded the subsequent behaviour of the resident spiders on audio cassette for later analysis. An interaction was deemed to have terminated when (1) one of the pair abandoned the web, (2) 30 min elapsed without courtship, or (3) copulation ceased. We captured 97 males and 93 females and immediately preserved them in 70% alcohol and glycerol for further examination. The remaining males and females were able to avoid capture. With a Kyowa binocular microscope we measured (to the nearest 0.25 mm) (1) length and (2) width of the opisthosoma (the rear portion of the body), (3) width and (4) length of the prosoma (the anterior portion of the body), (5) pedipalp length, (6–9) first, second, third and fourth leg length. Legs and palpal measurements were taken from trochanter base to tarsus tip. Body lengths were measured along the midline of the prosoma and opisthosoma; widths were taken across the widest points of these body sections. Indices of leg size (length leg $1 \times 2 \times 3 \times 4$) and body measurements (length \times width) were also calculated.

Female fecundity (egg numbers) was investigated by dissecting the female opisthosoma ventrally. We rehydrated the alcohol-preserved specimens using a physiological (200 mM NaCl, 11.8 g/litre) saline solution for 1 h. The egg contents of the opisthosoma were scraped out onto a microscope slide. Both mature (≥ 400 μm diameter) and

immature (< 400 μm) eggs were counted. A marked size differential was usually evident allowing easy classification.

In the analysis of frequency data in the prey size investigation, G -tests were used unless a cell fell below a value of 5, in which case the Fisher exact test was used. Principal components analysis (Frey & Pimental 1978) was used to investigate size assortment between pairs following correlation analysis of male and female morphological measures which proved unsuccessful in demonstrating size-assortative pairing. Non-parametric statistics were used with courtship and copulation frequency and duration data. Means are cited \pm standard error.

RESULTS

Description of Courtship and Mating

Females oriented to large prey introductions within an average of 48.44 ± 21.43 s ($N=53$). Data on frequency and duration of activities were unavailable for one observation. The mean attack latency for the female (interval between prey introduction and the female capturing the fly) was 140.50 ± 35.23 s ($N=53$). Males oriented within a mean of 113.83 ± 17.95 s ($N=53$) and the mean latency for males entering the web (prey introduction to male entry) was 158.20 ± 23.53 s ($N=53$). The male then wrapped the fly with his own silk. The female made a mean of 2.73 ± 0.26 ($N=37$; maximum 7) unsuccessful attempts to reclaim the prey. Nuptial thread spinning consisted of the male wrapping the prey item and continuing repeatedly across the space between the prey and the web strands, forming a multi-strand structure with the captured insect suspended between web strands. 'Prey stealing' and nuptial thread spinning behaviour usually resulted in the destruction of an area of the web spiral, the male 'clipping off' strands of the web and the mating thread being suspended across the hole thus produced. Nuptial thread formation was used to define the onset of courtship; any activity prior to this might be kleptoparasitic in nature. Males often plucked with their third pair of legs or tapped on the nuptial thread and other web strands with the first two pairs of legs. There then followed a complex series of movements of both animals back and forth across the web, in some interactions interspersed with periods of inactivity.

The male approached the female along the nuptial thread. If the female assumed the mating

Table I. The effect of prey size on courtship and mating success in *M. segmentata*

	Large prey	Small prey	Test of significance
Total	60	60	
Ignored ($N=60, 60$)	5 (8.3%)	17 (28.3%)	$G=8.40^{**}$
Captured by male ($N=60, 60$)	1 (1.6%)	2 (3.3%)	NS§
Captured by female ($N=60, 60$)	54 (90.0%)	41 (68.3%)	$G=8.89^{***}$
Removed by female ($N=54, 41$)	11 (20.4%)	34 (82.9%)	$G=39.38^{***}$
Flies remaining on web ($N=54, 41$)	43 (79.6%)	7 (17.1%)	$G=10.01^{**}$
Male entered web ($N=43, 7$)	43 (100%)	7 (100%)	
Male courted ($N=43, 7$)	37 (86.0%)	7 (100%)	NS§
Male copulated ($N=43, 7$)†	14 (32.6%)	6 (85.7%)	$P=0.035§$
($N=60, 60$)‡	14 (23.3%)	6 (10%)	$G=3.93^*$

†Frequency of copulations of those males that courted.

‡All prey introductions included.

§Fisher exact probability test.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

position by forming a loop around the nuptial thread with her third pair of legs the male could insert his pedipalp into the female epigyne through this loop. Attempted copulations occurred where full palpal insertions were attempted but not achieved. Copulation occurred as the pair were suspended from the web on the nuptial thread. Females did not feed during copulation. The average interval between prey introduction and the commencement of copulation (for large prey introductions) was 814.78 ± 105.97 s ($N=14$). The mean total interval between initial prey introduction and termination of copulation and the separation of the pair was 968.29 ± 108.49 s ($N=14$). Males seemed to terminate copulation by pushing against the female with their legs.

Effects of Prey Size

Female predatory behaviour varied with the size of introduced prey items (Table I). Of the 60 large and 60 small flies thrown into webs, fewer large prey items were left untouched by the female, compared to small prey. Only one large prey and two small prey were captured by males and in none of these cases did the male subsequently initiate courtship with the resident female. More large prey items were captured by females but significantly fewer of these were removed from the web to the off-web retreat. More large prey items, therefore, remained on the web available for male courtship initiation.

Initially, the size of prey introduced into the webs of female *M. segmentata* appeared to have a

marked effect on the mating activities observed. Male web entry, courtship and copulation (Table I) occurred significantly more often with large prey (43/60, 7/60, $G=48.25$, $P=0.0001$; 37/60, 7/60, $G=34.16$, $P=0.0001$; 14/60, 6/60, $G=3.93$, $P < 0.05$ for male web entry, courtship and copulatory behaviour, respectively). However, because the female sometimes removed the fly the male could initiate courtship after capturing a prey on only 43 occasions with large and seven with small prey (Table I). Males entered the female's web in all instances when the female did not remove the fly. In addition, only 37 males courted the female in the large prey group, of which 14 succeeded in mating, while courtship was observed in all the cases where small flies remained on the web but only six males mated (Table I). When this subset of data (flies remaining on web) were analysed, courtship was not more common in the large prey introductions (Table I).

Copulation durations for large ($N=14$) and small prey ($N=6$) introductions were not significantly different ($\bar{X} \pm \text{SE}$: large prey 153.52 ± 11.077 s, small prey 137.31 ± 17.3 s; Mann-Whitney $U=28$, NS). Frequencies and durations of each behaviour for copulating did not differ between small and large prey introductions.

Effects of Female Reproductive State

The number of mature eggs differed significantly where females were courted and copulated, were courted without success, and were not courted at

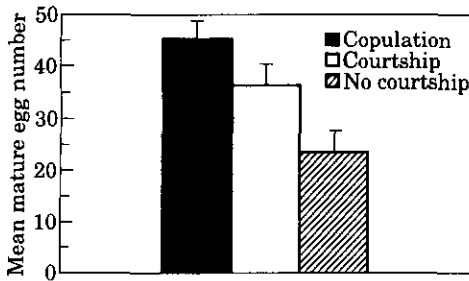


Figure 1. The influence of female reproductive status on male mating behaviour and success in *M. segmentata*. Error bars are standard errors. Data are for 14 copulations, 20 unsuccessful courtships and 16 cases where there was no courtship; 10 females escaped capture.

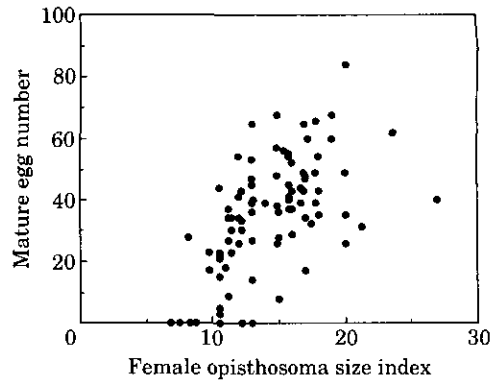


Figure 2. Opisthosoma size index (length \times width) in females in relation to mature egg load.

Table II. Correlations between indices of female size and female egg loads

		<i>r</i>	<i>P</i>
Leg index	Mature eggs	0.03	NS
Leg index	Immature eggs	0.19	NS
Leg index	Total eggs	0.26	<0.02
Prosoma index	Mature eggs	0.12	NS
Prosoma index	Immature eggs	0.08	NS
Prosoma index	Total eggs	0.27	<0.02
Opisthosoma index	Mature eggs	0.59	<0.001
Opisthosoma index	Immature eggs	-0.39	<0.001
Opisthosoma index	Total eggs	0.38	<0.001

N = 91 throughout.

all, in the large prey group (one-way ANOVA, $F_{2,49} = 7.18$, $P < 0.002$; Fig. 1). This also applied for total egg numbers (one-way ANOVA, $F_{2,49} = 4.00$, $P < 0.03$) but not to immature egg numbers.

There were several significant positive correlations between indices of female size and numbers of total eggs and mature eggs; and a negative correlation between opisthosoma index and immature eggs (Table II). In particular, the index of female opisthosoma size was positively correlated with mature egg load (Fig. 2). No significant relationships were recorded between indices of male size and female reproductive state (egg load). Copulation duration was positively correlated with female size, as expressed by the prosoma index ($r_s = 0.63$, $N = 14$, $P < 0.05$, Fig. 3a). Courtship duration was correlated negatively with female mature egg load ($r_s = -0.553$, $N = 14$, $P < 0.05$, Fig. 3b).

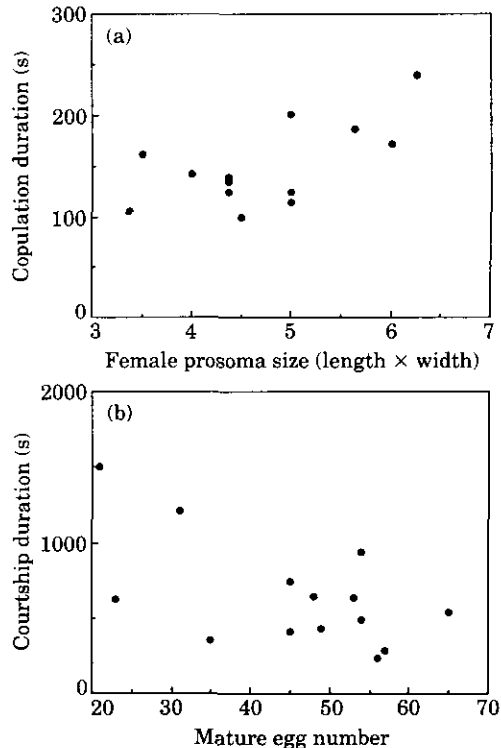


Figure 3. (a) Copulation duration in relation to female size (prosoma index) and (b) courtship duration in relation to female mature egg load.

There was no significant difference in reproductive status (mature egg number) between female spiders tested in the two prey size groups ($t = 0.80$; $df = 90$, NS; total egg number, $t = 0.37$, $df = 90$, NS).

Size-assortative Pairing

There were no significant correlations between any of the linear measurements of male morphology and those of females (including size indices). Principal components analysis, however, enabled the numerous linear measurements to be reduced to two factors for each sex. Factor 1 for females ('female leg length') loaded on lengths of legs one, three and four. Factor 2 ('female body size') loaded on prosoma and opisthosoma measurements. In males, factor 1 ('male size') loaded on measurements of opisthosoma, prosoma and lengths of legs one and three. Factor 2 ('pedipalpal length') loaded on male pedipalp length. The individual scores for these factors were then subjected to correlation analysis. There was a significant positive correlation between 'male size' and both 'female leg length' ($r=0.27$, $df=87$, $P<0.02$) and 'female body size' ($r=0.22$, $df=87$, $P<0.05$), indicating that size-assortative pairing occurs in this species although the correlations are weak. There was no size assortment among mating pairs, however.

Male Size and Mating Success

Mating success was not affected by male size in the large prey group. Relative size of males compared with females (male prosoma index/female prosoma index) also did not affect male success. Furthermore, there were no differences in either of the male PCA scores in males that did and did not mate. Neither courtship nor copulation duration was correlated with any of the three indices of male size.

Durations of Mating Activities

We examined the durations of activities using data for females that captured the large prey since few small prey were captured. Females that ultimately copulated captured prey significantly faster than those that were courted unsuccessfully and those that were not courted (29.2 ± 7.63 s, 121.1 ± 45.33 s and 265.7 ± 89.84 s, respectively; $F_{2,50}=3.63$, $P<0.05$). There was a negative correlation between the numbers of mature eggs and both the latency of female response to prey ($r=-0.324$, $df=48$, $P<0.05$) and prey capture ($r=-0.569$, $df=48$, $P<0.01$). Male copulation attempts were positively correlated with the frequency with which females assumed the loop position ($r_s=-0.519$, $N=12$, $P<0.05$).

DISCUSSION

Prey Size

Larger flies elicited more courtships and copulations than did small flies (Table I). There are a number of reasons for this. First, females ignored more small prey items than larger ones, suggesting that small prey often produce insufficient disturbance in the female's web to elicit predatory behaviour. Second, and most importantly, females were more likely to remove small prey, rendering them unavailable for use in male courtship. If these cases are excluded from analysis, however, there was no difference in male entry to the web, nuptial thread formation, attempted or successful copulations where prey was large or small. Blanke (1974) suggested that small flies did not produce web vibrations of a sufficient amplitude to elicit courtship. However, the present study suggests that small flies are removed by the female and that this prevents courtship.

Female Reproductive State

Female reproductive state, as determined by egg load, influenced courtship and mating behaviour (Fig. 1). In particular, females with few mature eggs were less likely to be courted. This might indicate that males are able to assess female quality. Alternatively, the male may be assessing the female's motivation to feed or her proclivity for predatory behaviour. Females that mated captured prey faster than other females and female response and prey capture latencies were negatively correlated with mature egg loads. Food intake affects fecundity in spiders (Wise 1979). More hungry, less fecund females might be expected to remove prey from the web and feed on it, whereas high quality, highly fecund females might be less inclined to do so (even to the point of ignoring prey altogether). However, the negative correlation between courtship duration and female egg load indicated that females with many mature eggs were more receptive to courtship (Fig. 3b). Shorter prey capture latencies in more fecund, guarded females, therefore, may also be indicative of willingness to mate. Furthermore, female willingness to mate is the most probable explanation of the success rate of males in small prey introductions (Table I), given that weights of the two fly groups did not overlap.

Any male assessment of female quality might be achieved by gathering information about the

weight or size of the female, or through a releaser pheromone produced by the female or a behavioural cue. The weight of female spiders correlates positively with egg number (e.g. Bristowe 1958; Wise 1979; Rubenstein 1987), as does female size (Petersen 1949; Table II and Fig. 2). Vibratory cues from the web may be the source of such information. Males, however, also appear to use pheromonal cues from the web to assess female reproductive state and to decide whether to guard or not (Prenter 1992). Such cues might also provide sufficient information for male spiders to decide whether or not to court. The small time difference between mean female prey capture and male web entry may imply that the male reacted to the arrival of the prey item rather than to the behaviour of the female. However, since the males reacted (oriented on the fly) to the disturbance in the web but waited for the female to capture the fly before entering the web, this is unlikely. At present, the specific information used by males in courtship and mating decisions is unclear. Apart from the male entering the web more quickly, courtship was shorter when the female had a large mature egg load. This may indicate a willingness on the part of larger, more fecund females to mate.

Copulatory Behaviour

Males copulated for longer with large females (Fig. 3a) and large females tended to have more mature eggs (Fig. 2). Thus, males may adjust copulation duration to female egg load. Longer copulations may increase the number of eggs fertilized as in the bowl and doily spider, *Frontinella pyramitela* (Austad 1982; but see Brown 1985; Christenson & Cohn 1988). The characteristics of the relationship between sperm transfer, copulation time and egg fertilizations in *M. segmentata* is unclear. The male appeared to terminate copulation. However, the correlation between fertilizations and copulation duration in another spider (Austad 1982) suggests longer copulations are highly advantageous.

Male *M. segmentata* insert a single palp at copulation, in contrast to the sequential insertions of both palps common in other spider species (e.g. Christenson et al. 1985; Elgar & Nash 1988; Elgar 1992). Damage or deformation of either the male's palp or the female's sperm-receiving organ or an assessment by the male of spermathecal obstructions such as a mating plug could explain the use of

a single palp (Watson 1988) in some males but not the unvarying use of a single palp by all males in the present study. If there is a first male advantage in fertilizations, injury to both pedipalps may be avoided during copulation with females of moderate reproductive quality (Watson 1988), for example, a non-virgin female. Other explanations may involve (1) the risk of cannibalism if a second palpal intromission is attempted (e.g. Elgar 1992) and (2) the conservation of sperm supplies by males. Watson (1991) showed that *Linyphia litigiosa* females bet-hedged by preferring multiple paternity for their broods. If females are selected to do this, then they would penalize males attempting to fill both spermathecae. The adaptive significance of the use of a single palp by males in mating is unclear and merits further investigation.

Size Assortment

Rubenstein (1987) found positive size-assortative pairing in *M. segmentata*. In the present study, size-assortative pairing was indicated by correlation analysis of principal factors from principal components analysis. Size-assortative pairing in arthropods might be brought about by a variety of means (Crespi 1989; Elwood & Dick 1990). In *M. segmentata*, it is likely to be due to aggressive competition between males for the largest and hence most fecund females (Rubenstein 1987). Rubenstein (1987) indicated a high degree of such competition, with large males tending to be more successful in obtaining and retaining large females. Size advantages in male agonistic interactions has been demonstrated for a variety of invertebrates (reviewed by Archer 1988; Elwood & Neil 1992). In other arachnid species (e.g. Watson 1990; Benton 1992), males compete for females and larger males have a competitive advantage. Here, females do not express mate choice with respect to male size. Large size in mating males is ensured by male-male competition during mate guarding. This may account for the apparent lack of female choice for larger males in *M. segmentata*. Size-assortative pairing probably leads to size-assortative mating in the autumn spider, by male-male and female-female competition (as suggested by Rubenstein 1987), rather than interactions between the sexes. Size-assortative mating was not found in the present study; however, this is not unexpected since size-assortative pairing was weak and, therefore, may have become non-significant with reduced

sample size. There is no indication, however, that size assortment facilitates mating. The size of the male relative to that of the female influenced neither the decision to court nor the success of courtship.

The Role of the Prey Item

The involvement of the prey item in the courtship and mating behaviour of *M. segmentata* is apparently not a male nuptial feeding strategy. Large prey did not enable males to engage in longer copulation, as theory predicts (Thornhill 1980), or achieve more matings and thus the use of prey appears dissimilar to nuptial feeding in some other arthropods. Indeed, females did not feed during copulation. Furthermore, males could not supplement the females' food intake by allowing them to consume captured flies. Non-mating females regained the fly after interaction with the male.

Some cost of courtship, reduced through selectivity, may explain the failure of males to court, even when a large prey arrived. This cost might be the risk of sexual cannibalism by unreceptive females. Sexual cannibalism of courting males can occur in *M. segmentata* (personal observation). Since sexual cannibalism is said to have been responsible for the evolution of the courtship behaviour of orb-web spiders (Elgar 1991), the inclusion of the prey item in the courtship behaviour of *M. segmentata* may owe something to the action of this strong selective force. By waiting until the female has captured a prey item before entering the web and initiating courtship, the male may reduce the risk of cannibalistic attack by the female (Prenter et al., in press).

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