

Patterns of mate guarding in *Metellina segmentata* (Araneae: Metidae)

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Summary

Mate guarding is a commonly reported phenomenon in spiders, but there are few detailed studies. Here, we describe the web population and patterns of mate guarding in the common orb-web spider, *Metellina segmentata* (Clerck), in a series of field investigations. A high turnover of males at webs of females was observed. Although virtually all females received a guarding male at some time, only one third to a half of females were guarded at any time. Females received numerous guarding males, whereas males rarely guarded more than a single female. A peak period for mate guarding by males was identified, with newly arrived males accounting for the majority of guarding males on a given day. Male movement between webs of females was greater in night-time hours. The mean duration of guarding was around half a day.

Introduction

Although male cohabitation with female spiders has been described (Ridley, 1983; Jackson, 1986), there are few detailed studies of mate guarding in spiders (Toft, 1989). The autumn spider, *Metellina segmentata* (Clerck) (Araneae: Metidae), is common and widespread throughout Great Britain and Ireland from late summer to early autumn (Roberts, 1985). This species has a strictly annual life cycle (Toft, 1983) and mating, which depends on the arrival of a prey item of a certain size (Blanke, 1974; Prenter, Elwood & Colgan, in press), occurs from September to October. Before mating, males guard the webs of females and defend their position against rival males searching for mates (Blanke, 1974; Rubenstein, 1987; Prenter *et al.*, in press), leaving after mating. There are thought to be high rates of male turnover (Bristowe, 1958) and a 3–4 week period of precopula guarding (Rubenstein, 1987).

Mate guarding is an adaptation that increases the chances of a male mating successfully (Ward, 1984; Toft, 1989). Precopula mate guarding may evolve through frequency-dependent selection as a result of a male-biased operational sex ratio (OSR) (Emlen, 1976; Emlen & Oring, 1977; Grafen & Ridley, 1983), possibly coupled with a priority in fertilisations of the sperm of the first male to mate with a female. Males should mate guard only when the estimated benefits exceed the costs. If the costs exceed the benefits, a female should be rejected. Higher costs may be associated with mate searching compared with mate guarding, as mortality rates in searching males are higher than in guarding males (Vollrath & Parker, 1992). Size of individuals, both absolute and relative, may influence these costs and

benefits (Elwood & Dick, 1990). For example, small male *M. segmentata* are more likely to be ousted in male–male agonistic interactions and the smaller males are more likely to be cannibalised by the female at this time (Rubenstein, 1987). Assessments and decision-making in mate guarding by male autumn spiders have been discussed elsewhere (Prenter, 1992). The present study describes the structure of the web population of *M. segmentata* and investigates mate guarding by direct observation and experimentation, in the field.

Materials and methods

Web populations

The study was conducted at Murlough National Nature Reserve, Dundrum, Co. Down (grid ref. J 414 352), approximately 30 km south of Belfast. Daytime surveys of the web population of *M. segmentata* on gorse bushes were carried out on 23 September 1988, 15 September 1989, 20 September 1990 and 23 September 1991 between 1000 and 1400h. Approximately two webs were selected randomly on each bush. The sex of the residents and the presence of associated individuals were recorded.

Potential for male arrivals

The webs of 18 females were chosen randomly, marked and monitored twice daily (at approximately 12 h intervals, between 0600 and 0900, and 1700 and 2100) from 1 September–9 October 1991. The webs were situated on different bushes over a range of 400 m. Males observed in cohabitation were removed, weighed, restrained on a petri dish with a mm² background using the up-turned lid, measured from coxa to tip of the first leg, and later released away from the study area. Hour-long observations of different webs ($n = 51$, 25 solitary females, 26 guarded females) were also conducted in daylight (between 1000 and 1400h), during which the arrival of males and prey items was recorded.

Seasonal mate guarding survey

The webs of 73 females on a line of isolated bushes approximately 300 m long were marked and monitored twice daily (as above) from 9 September–9 October 1991. Males were carefully removed, measured (as above), individually marked with a small spot of Tipp-Ex[®] and replaced at the web. The presence of previously marked males was also recorded on these webs. Females were not marked. Some males escaped capture.

Results and discussion

Web populations

The results of the four surveys are presented in Table 1. A high proportion (range 79–91%) of males were observed in cohabitation with a female (Table 1). In contrast, only 33–56% of females were guarded. The proportion of males in cohabitation was most probably

an overestimation, given the difficulty of observing solitary males off webs. Many males may have been hidden in vegetation and, therefore, the number of males in the population must be regarded as an underestimate.

The number of solitary males and females, paired males and females, and females guarded by two males differed significantly over the years (G-test (4×4), $G = 34.48$, $p < 0.0001$; Table 1). More females were guarded in 1990 and 1991. The proportion of males guarding during the surveys (Table 1) was consistent between years (G-test (4×2), $G = 6.43$, $df = 3$, NS), but the proportions of females guarded differed ($G = 22.24$, $df = 3$, $p < 0.0001$). Without more detailed data on the prevailing ecological factors, it is difficult to attribute these changes to specific factors. However, these results indicate a fluid pattern of mate guarding and variation in the overall breeding population structure of *M. segmentata* from year to year. All the surveys were conducted at approximately the same time of the year and, therefore, at similar stages of the life cycle and mating season of *M. segmentata*. Overall, the proportion of guarded to solitary females increased from 1988 to 1991. Male:female sex ratios, as determined by the survey of webs (Table 1), suggest a female-biased sex ratio, in concordance with the predictions of Vollrath & Parker (1992). However, as indicated above, the number of males in the population was undoubtedly underestimated.

Potential for male arrivals

Seventy-two males were observed guarding females on the 18 marked webs. Initial male arrivals were recorded on 10 ($n = 8$), 11 ($n = 2$), 12 ($n = 1$), 13 ($n = 2$), 15 ($n = 3$), 16 ($n = 1$), and 17 ($n = 1$) September 1991. By removing males, occurrences of males encountering webs and deciding to move on, or being forced off in agonistic interactions were minimised. Each female received a mean of 4.0 (SE = 0.75, $n = 18$) males over the study period. The mean interval between arrivals of males was 2.75 ± 0.40 days ($n = 60$). Average male weight was 24.48 ± 0.82 mg ($n = 71$).

Male weight was correlated negatively with the day in the survey when a male was recorded (Fig. 1). However, measurements of size did not decline with time in season, e.g. first leg length ($r = -0.1$, $df = 69$, NS). These results suggest that males arriving to guard at the webs of

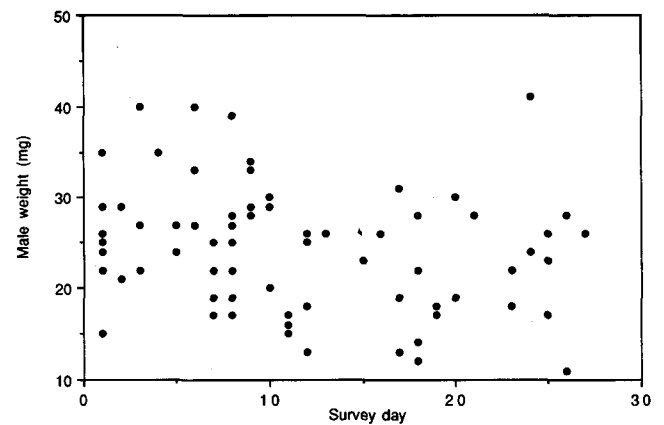


Fig. 1: Observed weight reduction in males arriving to cohabit with females on webs as the male removal from the 18 webs of females continued. Day 1 was 9 September 1991 ($r = -0.24$, $df = 69$, $p < 0.05$).

females became progressively lighter over time. A number of explanations may account for this: (1) The data may reflect the influence of male-male agonistic interactions, with larger males winning fights over newly moulted females at the start of the mating season but being less persistent in the defence of previously mated or lower quality females towards the end of the season. Such an explanation is dependent, however, on larger males depleting their sperm supplies in mating with these virgin females. Sperm depletion in matings with virgin females has been observed in the golden orb-weaver, *Nephila clavipes* (Linn.) (Christenson, 1989). *N. clavipes* males mating with older virgin, or mated females, only transferred a portion of their sperm load to the female (Christenson & Cohn, 1988). (2) Later, smaller males may represent later emerging and maturing, smaller males. (3) Smaller males may persist in the population longer; larger males may die of starvation earlier than smaller males as a result of greater energy expenditure. (4) The reduction in male weight may indicate a decrease in male weight through starvation, initiated by cessation of predatory behaviour and increased sexual behaviour in adult compared with juvenile males. Although spiders show adaptations to low food supplies (Austin & Anderson, 1978), movement between webs and the added exertions of courtship and mating activities, even where males gain some food while guarding females, are likely to result in weight losses in males

	1988	1989	1990	1991
M	14 (4.7%)	12 (6.4%)	15 (10.1%)	13 (5.4%)
F	185 (61.9%)	117 (62.2%)	79 (53.0%)	105 (43.2%)
MF	97 (32.4%)	53 (28.2%)	52 (34.9%)	114 (46.9%)
MMF	3 (1.0%)	6 (3.2%)	3 (2.0%)	11 (4.5%)
%F Guarded	35.1	33.5	41.0	55.9
% M Guarding	88.0	84.4	79.5	91.3
M:F	1:2.4	1:2.3	1:1.8	1:1.5
Total	299	188	149	243

Table 1: Structure of the population of *M. segmentata* associated with webs at Murlough N. N. R. surveyed on one day in each of four years, indicating solitary males (M), solitary (F) and paired (MF) females, including females with two attending males (MMF), percentage of females guarded, percentage of males guarding, and sex ratio. Two instances of a male with two females (one each in 1989 and 1991) and one instance of two females on the same web without a male (1988) are omitted.

during the mating season. The reduction in male weight was not associated with reduction in average male first leg length, suggesting that overall male size was not reduced concomitantly. (5) Experimental removal of larger males of high competitive ability may have provided an opportunity for smaller males to replace larger males at webs from which ordinarily they were excluded by virtue of their relatively inferior competitive ability.

During the hour-long observations, two males arrived at the webs of solitary females and one at a guarded web. Ten prey items were intercepted; six by solitary females and four by guarded females. Although prey items are involved in the courtship and mating behaviour of autumn spiders (Bristowe, 1958; Blanke, 1974; Prenter *et al.*, in press), no matings occurred. This gives an average of one male arriving at a web every 17 h and one prey item every 5 h during daylight.

Seasonal mate guarding survey

Male arrivals and guarding activity were most evident between 15 September and 2 October (days 7 and 24; Fig. 2a). The dramatic drops in male guarding and arrivals during the 18-day peak activity period were due to strong winds and heavy overnight rain. Nyffeler & Benz (1989) suggested that *M. segmentata* is mostly active during daylight hours; however, more males arrived to cohabit in the morning compared with the evening (Wilcoxon, $z = -4.42$, $p < 0.0001$, $n = 31$ days; Fig. 2b). This most probably reflects a preference of males to move during darkness, although movement during daylight hours was still evident. Nocturnal bias in male movements could reflect predator avoidance, or an attempt to arrive at webs when females are less active and, therefore, less likely to attack.

During the peak guarding period, an average of 20.67 ± 1.89 (range 6–30) of the monitored webs were guarded on any day, i.e. $28.31 \pm 2.59\%$ (range 10–50%) of webs were guarded per day. This average value is similar to the percentage of guarded webs in the web surveys for one day in each of four years (Table 1). On any given day, newly arrived males accounted for most males guarding (Fig. 2a). This illustrates the peripatetic nature of the male lifestyle and the continuous flux throughout web sites in the population studied. Overall, 281 males were observed in cohabitation at the 73 webs. The mean inter-male arrival rate at webs was one male every 1.69 days (± 0.14 , $n = 384$). Male tenancy ranged from a minimum of 0.5 days to a maximum of 4.0 days. The average cohabitation duration for males was 0.66 days (± 0.4 , $n = 462$). The distribution of male tenancy is presented in Table 2.

Male first leg length ($\bar{x} = 16.09 \pm 0.12$ mm, $n = 228$) was negatively but weakly correlated with the day in the

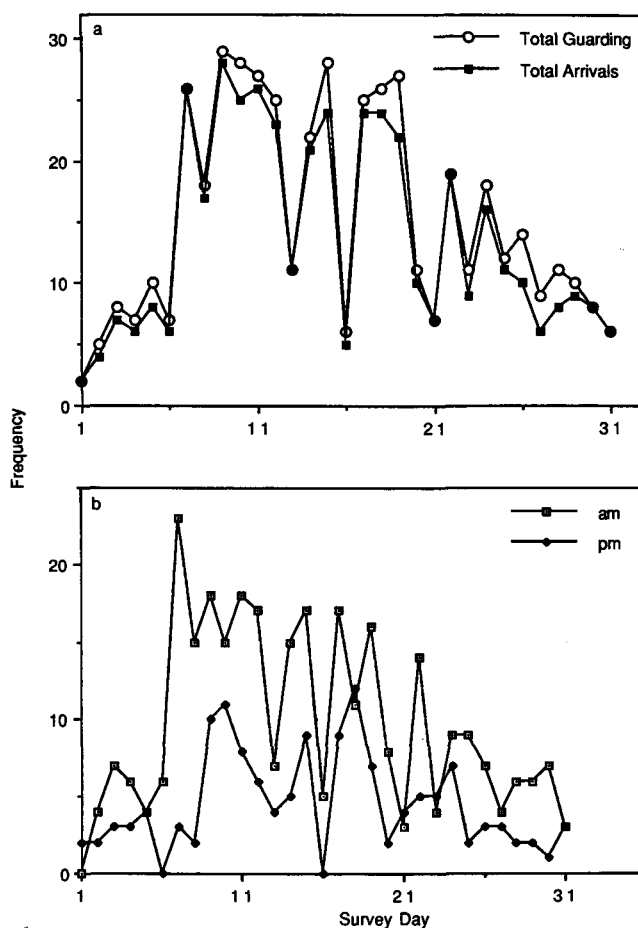


Fig. 2: (a) Frequency of male arrival and the number of webs guarded during a survey of mate guarding at marked webs observed throughout the season. Day 1 was 9 September 1991. On any one day, new arrivals accounted for the majority of males guarding. (b) Male arrivals on webs of females in the morning and afternoon. More males were observed to arrive in the morning compared with the afternoon.

survey when the male was first observed ($r = -0.194$, $n = 228$, $p < 0.05$); most males were not encountered repeatedly. Since males were not removed from webs, this might reflect either a deterioration of male quality as a result of starvation as the season progressed, or later maturing males that never achieve the size of larger, earlier maturing males. Maturation and the initiation of mate searching in males may be size dependent.

Marking did not affect male survival or behaviour. This was assessed by comparing the first and second cohabitation durations of males that guarded two females ($n = 65$). Mean durations of first (0.63 ± 0.27 days) and second (0.66 ± 0.49) cohabitations were not significantly different (Wilcoxon, $z = 0.152$, NS). If the marking had a deleterious effect, the first guarding duration would be expected to be significantly shorter than the second.

Cohabitation duration did not vary with male size ($r = 0.106$, $n = 245$, NS). Males attended an average of

Cohabitation duration (d)	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Frequency	369	71	11	6	2	1	1	1

Table 2: Frequency distribution of cohabitation durations for males observed on 73 female webs from 9 September–9 October 1991.

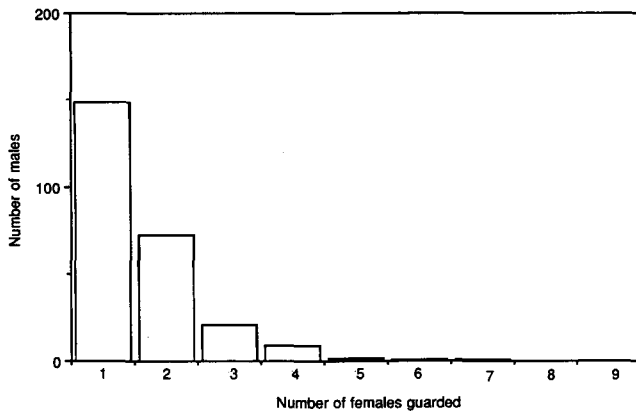


Fig. 3: Distribution of the number of females guarded per male (9 September–9 October 1991).

1.64 ± 0.9 (mode = 1) webs, but the majority of males guarded only one female (web) (Fig. 3). Males that failed to guard any females could not be recorded with the method employed. The number of webs and hence, females, a male attended increased significantly with male size (ANOVA, $F = 2.601$, $df = 4, 227$, $p < 0.04$; Fig. 4). Post-hoc tests (Fisher PLSD) indicated that the significant differences were between the males that cohabited with 1 and 4 females ($p < 0.05$) and males that cohabited with 2 and 4 females. The positive trend towards increasing male size with increasing number of cohabitations made by these males (Fig. 4) suggests that large males attended more females and hence acquired more copulations than small males. These results concur with those of Rubenstein (1987) who found that larger males were capable of monopolising aggregations of large females.

To test the prediction that males encountering more females will guard for shorter durations (Grafen & Ridley, 1983), the average cohabitation durations of males that attended 1 to 5 or more females were compared (Table 3). There was a significant difference in the average cohabitation durations of males in these groups, but there was no trend for males that guarded more females to guard for shorter periods of time.

During the survey, 5 males were observed in courtship. A further 5 males were found dead in the webs of females. Webs with two males guarding were observed on 34 occasions and one web had three males in attendance. The distribution of males attending (received by) each female is shown in Fig. 5. Five females were not guarded at all.

No. females guarded	n	Mean guarding duration (d)	SE
1	149	0.63	0.04
2	65	0.66	0.04
3	20	0.63	0.03
4	9	0.71	0.07
≤5	4	0.66	0.10

Table 3: Comparison of average cohabitation durations of males that guarded different numbers of females (Kruskal Wallis, $df = 4, 247$, $H = 19.79$, $p < 0.001$).

There was an initial rapid decline (approximately 80%) in numbers of males guarding for more than 0.5 days (Table 2). The rate of decrease in males remaining at the webs of females continued at a similar rate up to 1.5 days. The number of males remaining was further reduced by approximately 50% per half day in subsequent days.

General discussion

The various investigations of mate guarding in the autumn spider, *M. segmentata*, presented in this study, suggest a fluid pattern of mate guarding, where adult males wander through the population of webs built by females. Approximately one third to one half of the webs of females surveyed had a guarding male on a given day. These data agree with the sex ratios determined in the web surveys conducted from 1988 to 1991 (Table 1), but these surveys underestimated the density of males because males off webs could not be monitored.

Problems associated with monitoring male movements are further illustrated in variation in the estimates of inter-male arrival intervals. These arrival intervals affect estimates of the number of females guarded by males and the number of males received by females. Male turnover was estimated as one male every 2.75 days (66 h) when males were removed to avoid interaction between resident and newly arriving males. Webs monitored over 31 days without removal of males suggested an estimated turnover rate of one male every 1.69 days. Local depletion of males may have contributed to the lower turnover rates when males were removed from webs (and the study area). There are also limitations inherent in the twice-daily recording regime. Males might come and go without being detected. In contrast, the daylight one-hour surveys gave a higher estimate of one male every 17 h. It is not clear, however, whether these males remained to guard females for any length of time, and the true turnover rate may be lower than one male per 17 h. However, because male movement increased at night (Fig. 2b), overall male turnover rates are likely to be greater at night than during daylight.

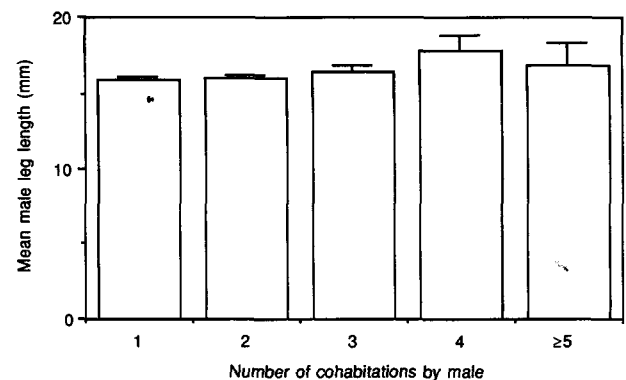


Fig. 4: Relationship between male size, measured as first leg length (mm), and the number of webs/females attended by males. Means for males that cohabited with five or more females were lumped together. The five groups contain data on 134, 63, 18, 9 and 4 males for 1, 2, 3, 4, ≥5 cohabitations respectively.

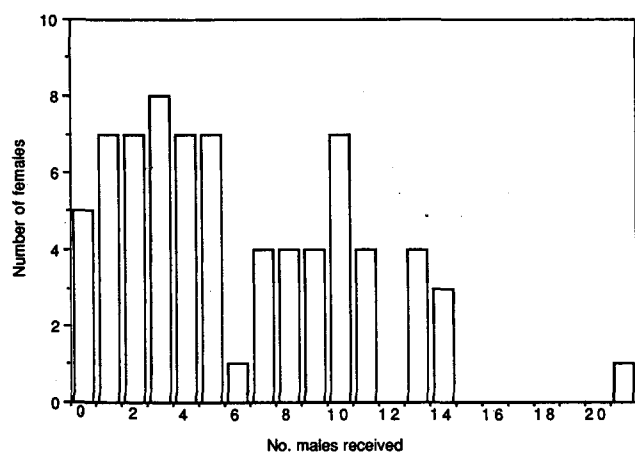


Fig. 5: Frequency distribution of number of males received by females over the survey period 9 September–9 October 1991.

Large males guarded more females. Smaller males, therefore, may spend more time solitary, as a consequence of abandoning webs encountered that are already occupied by larger males, or being ousted more often in agonistic encounters. This suggests strong selective advantage for large size in male spiders. Alternatively, S. E. Riechert & F. D. Singer (pers. comm.) found that large male *Argiope aurantia* Lucas (Araneidae) moved further than small males and may, therefore, obtain more matings. These authors found a preference for females to mate with relatively larger males. The guarding behaviour observed in *M. segmentata* is consistent with the precopula guarding described in the bowl and doily spider (*Frontinella pyramitela* (Walckenaer)), where cohabitation duration is short (Suter & Walberer, 1989). Male *M. segmentata* prefer more fecund females, both at the initiation of guarding (Prenter, 1992) and in courtship and mating behaviour (Prenter *et al.*, in press).

Male cohabitations were characterised by short tenancies, and the pattern of male abandonment of webs (Table 2) suggests similarities with the stochastic behaviour of bowl and doily spiders (Suter & Walberer, 1989; Suter, 1990; Suter & Sanchez, 1991). Before this situation can be considered further, however, the influence of female reproductive status and additional ecological factors on male guarding behaviour require examination. The need for a suitably sized fly to be captured for courtship to be initiated by guarding male *M. segmentata* (Blanke, 1974; Prenter *et al.*, in press) may be an important random element which determines the guarding behaviour of males. Males leave webs after mating (Prenter *et al.*, in press), others will be ousted in agonistic interactions (Rubenstein, 1987; Prenter, 1992) and others may give up if suitable prey are not available.

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