

## Alternative reproductive tactics in the spider *Meta segmentata*

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**Summary.** In the spider *Meta segmentata* web site quality and competitive ability determine female distributions, and ultimately male mating strategy. Large, fecund females position their webs in aggregations in high quality habitats, whereas small females live alone in lower quality sites. Competition for web sites is intense. Large females have a fighting advantage, but web ownership can offset size disadvantages of about 10%. Males compete for access to female webs. The smallest males are excluded from aggregations of females but have a very high probability of mating monogamously with females in poor habitats. The largest males move about within aggregations and by mating with many females achieve the highest reproductive gains. Moderately sized males only have a low probability of mating in an aggregation, but for those that do succeed the reproductive gains are higher than for those that mate monogamously in low quality areas. On average, moderately sized males obtain reproductive gains from the high risk, high gain strategy of defending webs in aggregations that are equal to those from defending solitary females in poor areas. That 18 of 21 moderately sized males defend females in aggregations suggests that *M. segmentata* behaves in a risk-prone fashion.

### Introduction

In many species competition for mates is intense. As a result, some males adopt different, and often less competitive, mating tactics. While some males defend territories, or advertise for females, others attempt to gain access by lurking silently nearby (e.g. frogs, Emlen 1976; Davies and Halliday 1978;

Howard 1984; Fairchild 1984; e.g. spiders, Christenson and Goist 1979), or even by mimicking the behavior of females (e.g. sunfish, Dominey 1980; Gross 1982; and gartersnakes, Mason and Crews 1985). Alternatives such as these will persist only as long as they yield reproductive benefits that exceed costs. Whether or not they do so depends on ecological and social circumstances. The purpose of this study is to determine what ecological and social conditions induce males of the orb-web building spider *M. segmentata* to select habitats that either produce meager reproductive benefits (monogamy) with virtual certainty, or offer the prospects of higher benefits (polygyny) with substantially less certainty.

Most research on alternative mating strategies has focused on two issues. One concerns the control of tactics and whether they are driven by genotypic or phenotypic differences (Austad 1984; Cade 1981, 1984). The other concerns pay-offs and whether tactics represent equally successful alternatives or responses of 'last resort' that produce rewards only sufficient for persistence (Rubenstein 1980; Cade 1980; Davies 1982; Dunbar 1982). While this study also evaluates these two aspects of male mating behavior in *M. segmentata*, the study is primarily designed to examine the mating systems as a whole in order to determine how ecological and social conditions shape the competitive behavior of males. Since differences with respect to sex, size, nutritional state, and past experience, will affect the needs and abilities of individuals in natural populations, I will focus on how intra- and inter-sexual relationships are shaped by the environment.

### Methods

*M. segmentata* is a sexually dimorphic species of spider in which females are only slightly heavier than males. Females build small orb webs (15–20 cm diameter) on low bushes and shrubs

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throughout the British Islands. Spiders are active throughout both day and night, but most web-building and repair occurs after dark.

Spiders were observed on hedges, garden shrubs, and window frames, in Grantchester, England. Over 200 males and 200 females were captured during the summer of 1979. After CO<sub>2</sub>-anesthesia, individuals were marked on the abdomen with fast-drying acrylic paint and had the width at their cephalothorax measured using a microscope fitted with an ocular micrometer. Marking seemed to have little effect on behavior since only 4 (<2%) individuals abandoned their initial website within one hour of being returned.

Early each morning a census was taken of the entire population. At this time all new, and recently molted adults, were captured, marked, and measured. In the few instances where sub-adults were inadvertently marked, exuvia were recovered from the web of the freshly molted adult and the same series of marks were re-applied. Half hour behavioral observations were made on randomly chosen focal individuals. During this period all feeding, web-building, agonistic and sexual behavior were recorded. When interactions occurred, the identity of the interactants and the sequence of behavior was recorded. After every two focal observations the study area was censused. A headlamp covered with transparent reddish plastic was used for the nocturnal observations.

All prey species caught in the web were identified and relative frequencies of capture were computed. Some webs were enclosed with plastic coated screen. By experimentally altering prey densities, the assessment capabilities and migratory behavior of *M. segmentata* could be monitored.

Manipulative experiments to measure competitive ability were performed by first collecting, measuring, and marking wandering spiders. Then they were released within 50 cm of the edge of the web of a particular spider to be tested. Only about 40% of these released spiders found the web. When they did every event in the interaction was recorded from the time of web entry until one of the spiders left the web. Some resident female spiders had their weight altered by gluing one or more 0.1 gm pieces of wire to their backs.

Shortly after the start of the mating season, a sample of copulating females and males from outside the study area, but from similar habitats, were collected and preserved in 70% ethanol. Later, comparisons of the cephalothorax widths of pairs were used to evaluate the prevalences of assortative mating. Females were also dissected to determine clutch size and the extent to which it is influenced by body size, habitat and diet. Standard parametric statistics were used throughout the analysis.

## Results

Mating systems are determined by male responses to female distributions and behavior. Consequently, the factors affecting female competitive relationships and distributions are examined first since they ultimately affect male mating behavior. This is clearly the case in *M. segmentata*: whereas adult females build webs; males either wander, or reside in the corner of a female's web.

### *Female behavior and distributions*

Two factors associated with foraging efficiency – prey availability and web longevity – determine

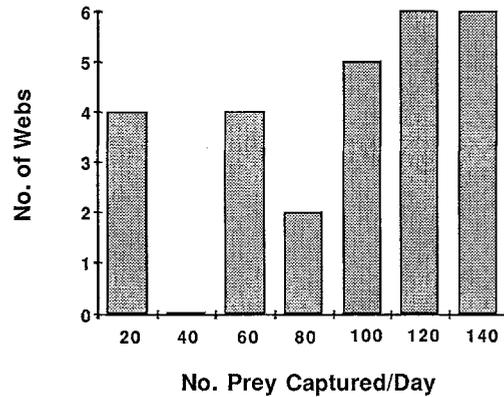


Fig. 1. Frequency distribution of daily web catching rates

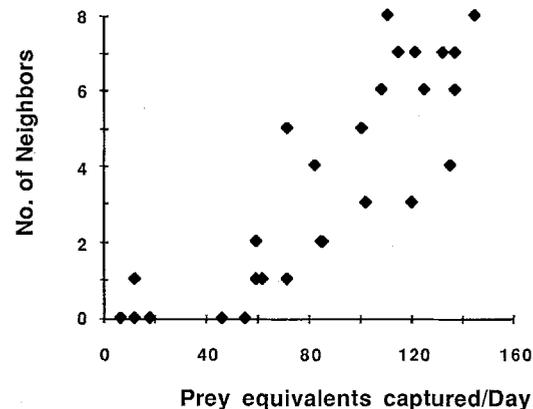


Fig. 2. Correlation between daily prey capturing rates and number of neighboring webs within 1 meter ( $r=0.86$ ,  $n=27$ ,  $P<0.01$ )

the distributions of female webs. The low bushy habitat is patchy and structurally diverse and this leads to spatial variability in the abundance and diversity of insects. As a result some webs are well protected by surrounding branches and leaves, whereas others capture large numbers of prey. To measure web quality I used an index that was the product of hourly capture rate and the number of hours per day that the web was extant and functioning. Since webs being reconstructed cannot capture prey, spiders living in habitats where webs are easily destroyed, or with a tendency to re-build frequently partly damaged webs may be at a foraging disadvantage. In order to make the foraging rate sensitive to differences in prey size, capture rate was scaled for prey size:  $\frac{1}{2}$  point was scored for prey smaller than 0.5 mm and 1 point was scored for prey larger than that size. The foraging success of a random sample of spiders from a variety of habitats was monitored (Fig. 1), and the differences among web-sites is large. Some sites cap-

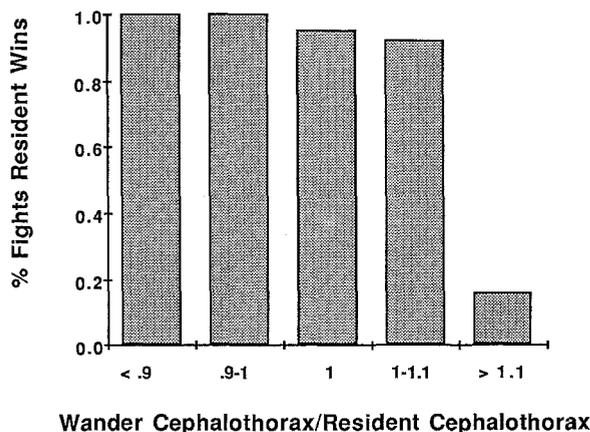


Fig. 3. Effects of residency and relative body size (wanderer cephalothorax width/resident cephalothorax width) on likelihood of females winning contests

tured more than 10 times the number of prey per day than other sites. In general webs placed in the corners of window frames, especially those through which little light passed, caught the least prey. The most productive webs were those out in the open, or those in areas where wind eddies often entrapped hundreds of small insects (Rubenstein, unpubl.).

Web site quality has a profound affect on the distribution of females. The sample of females used to measure web site quality was also used to count the number of webs positioned within 1 meter of the focal female's web. As Fig. 2 shows, females aggregate their webs in areas that have the highest daily yield of insects. Once capture rate drops below 60 prey equivalents per day aggregations rarely develop. When a web normally receiving between 75–100 prey equivalents was enclosed by

screening and all the natural prey was removed, 9 out of 10 spiders could be induced to leave the web and scurry about the screening if only 3 *Drosophila* per hour for 10 h were added to the enclosure. If 10 *Drosophila* per hour were added, however, all 10 spiders remained on their webs. Throughout this study sites with capture rates falling below this threshold (60 prey/day) will be classed as 'poor' or 'low' quality sites whereas those above the threshold will be classed as 'good' or 'high' quality sites. Window frames and small gaps in hedges usually constituted poor sites, whereas small shrubs in the open understory, or on large overhangs in light gaps were associated with good sites. It is interesting to note that in Fig. 2 the scatter (e.g. variance) in the number of neighbors increases as the site quality increases, suggesting that in some good areas either physical features or competitive abilities of certain females, limit the number of spiders that otherwise could be supported there.

Competition among females for web sites is common. When webs are destroyed by wind or rain, females usually rebuild them. Some do not, however, and wander in search of new web-sites. Of 22 marked females that abandoned webs without provocation by conspecifics, only 7 (30%) built their next web in an unoccupied site. The others challenged and ultimately displaced females already occupying webs. The length of these contests was affected by habitat quality. For equal sized pairs of competitors, contests occurring in high quality habitats were significantly longer ( $\bar{x} = 12.6$  min) than those in low quality areas ( $\bar{x} = 8.1$  min) ( $t_{41} = 2.11$ ,  $P < 0.025$ ).

Figure 3 shows that larger female spiders have a competitive advantage, but that a significant resi-

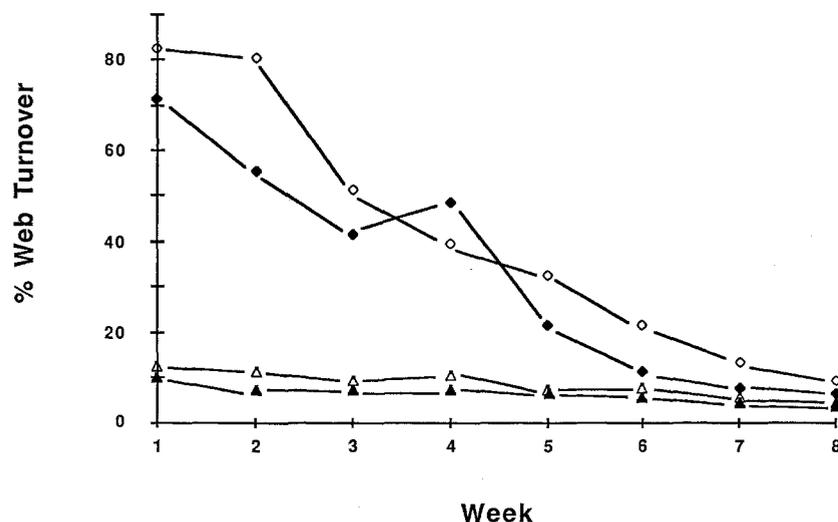


Fig. 4. Percentage of web ownerships that turnover per week (○ = males good habitat; △ = males poor habitat; ● = females good habitat; ▲ = females poor habitat)

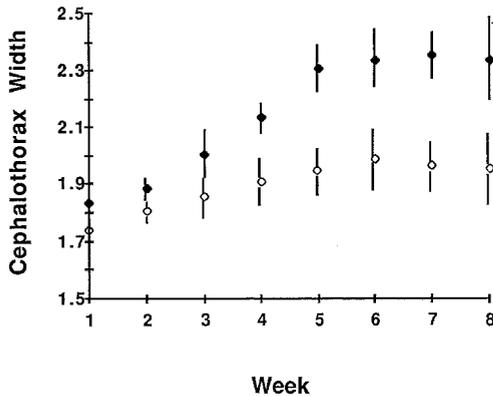


Fig. 5. Size of female web occupants ( $\blacklozenge$  = good habitat;  $\diamond$  = poor habitat; mean  $\pm$  SE)

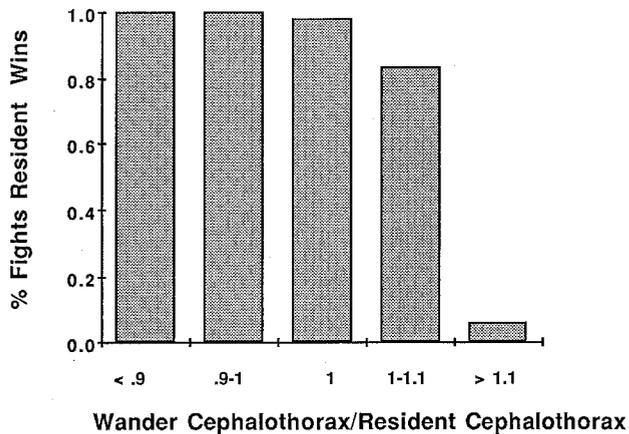


Fig. 6. Effects of residency and relative body size (wanderer cephalothorax width/resident cephalothorax width) on likelihood of males winning contests

density affect exists. When opponents are equal in size, the resident wins 95% of the encounters, and even when the resident is 10% smaller than the intruder it still wins 92% of its encounters. Only when the resident is much smaller (>10% difference) will it usually be forced (88%) to relinquish its web. Twenty vanquished residents had their weight artificially increased by 25% when wire strips were glued to their backs. When released in the vicinity of their old web, 19 attempted to reclaim them and 17 (89%) were successful.

Size related female-female aggression has two effects: One is on turnover in web ownership. Figure 4 shows that early in the season when adults first emerge, changes in ownership are common, especially in the high quality areas. By mid-September turnover rates are much lower, averaging about 10% per week, and no difference exists between high and low quality areas. The other is on the size distribution of female residents. In

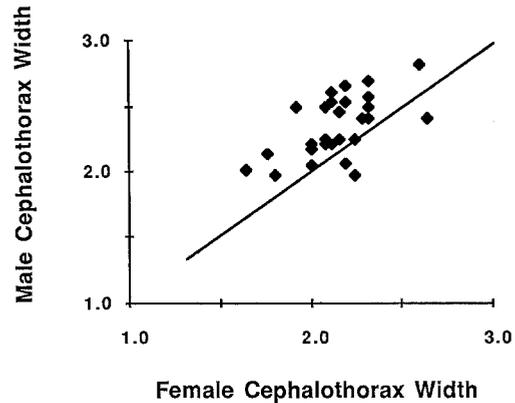


Fig. 7. Cephalothorax widths of paired males and females. Line represents pairs in which males and females are equal in size

order to displace a resident, a wanderer must be at least 10% larger. As a result, the size of the resident at any given site should increase as the season progresses. This is indeed the case (Fig. 5), especially in the best foraging areas. Interestingly a plateau is reached at about the time mating occurs. It appears that by the time the mating season commences the largest females are in large aggregations in the best foraging areas. This distribution and lack of turnover suggests that once egg-laying commences few large females are moving about and contesting occupied webs.

#### Male behavior

One of the interesting features about the mating behavior of *M. segmentata* is that males tend female webs prior to courtship. For 3-4 weeks before copulation males can be found in the corners of female webs. In the high quality, high density areas, more than one male may co-habit with a female, but only until one male assumes dominance and drives the others away. Aggression among males is common and experiments in which wandering males of particular sizes were released near residents of known sizes, show that larger males have a considerable fighting advantage (Fig. 6). To some extent this size advantage can be offset by the effects of prior residency since resident males who are less than 10% smaller than their opponents can still win 83% of their encounters. Nevertheless, the size of males at any given site increases as the season progresses (Fig. 5).

Since the same size shift occurs for both males and females, it is not surprising that positive size assortative mating occurs (Fig. 7). This suggests that males select the largest females in an aggregation and attempt to defend them for as long as

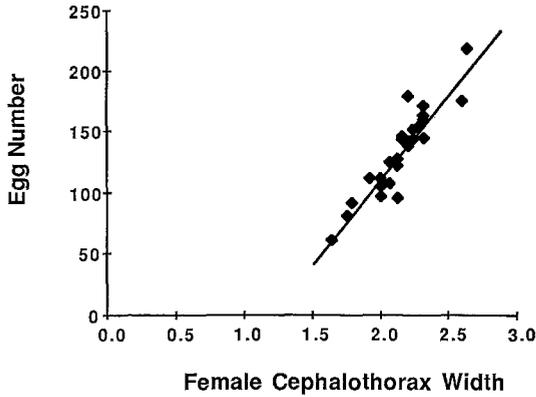


Fig. 8. Relationships of female size on number of mature ovarian eggs [regression egg number =  $-177.3 + (144.1) \times$  (cephalothorax width);  $r^2 = 0.85$ ,  $n = 26$ ,  $P < 0.001$ ]

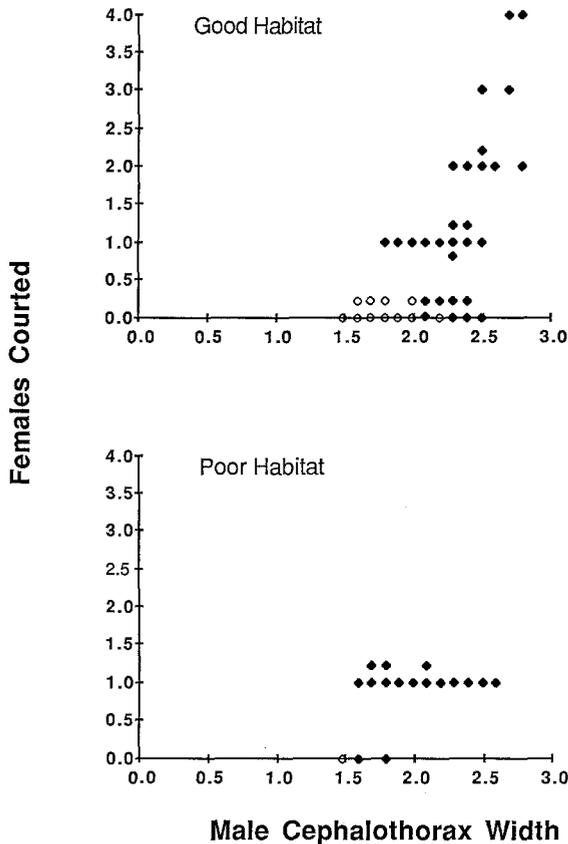


Fig. 9. Relationship between the number of females courted and male size in high and low quality habitats. *Filled circles* denote surviving males while *open circles* denote males who were cannibalized by females on the web during courtship

possible. If they are displaced prior to courtship they move on, challenging other males until they can displace one. Consequently, they mate with the female the previous male was guarding. Since male turnovers are somewhat more frequent than

those of females, even at the end of the breeding season (Fig. 4) the sexual dimorphism among pairs should generally increase as the season progresses ( $\delta > \delta$  in cephalothorax width). Exceptions occur, and Fig. 7 shows four instances in which males mated with females that were much larger than themselves. Thus it is possible for small males to escape combat with larger males and mate with disproportionately larger females. Although uncommon (14%), such copulations would prove to be reproductive bonanzas since female fecundity is highly correlated with female size (Fig. 8). Whereas as a male with a 2 mm wide cephalothorax could expect on average to mate with a female producing 80 eggs, one male with a 2 mm wide cephalothorax did mate with a disproportionately large female who was carrying 160 eggs.

#### Alternative male strategies

From a male's perspective the largest aggregations of females contain the largest females and thus represent areas where reproductive gains are potentially high. But it is in these areas that the likelihood of being displaced is greatest (Fig. 4), at least for the smaller males. Males found wandering are on average significantly smaller than residents ( $\bar{x}_{\text{wanderers}} = 2.12$ ,  $\bar{x}_{\text{residents}} = 2.36$ ;  $t_{38} = 2.97$ ,  $P < 0.005$ ). Displacements can be extremely costly since contests occur on a female's web. As males jockey to and fro a female lurks nearby ready to pounce upon, and cannibalize, any male that retreats too close to her. Since resident small males are most likely to be engaged in long escalated contests they incur the greatest risk of falling prey to resident females (Fig. 9).

Even if a small male manages to maintain its position in an aggregation, he may not be able to realize the potentially large reproductive gain. Although small males may share a web with a well fed female capable of laying more eggs than an equivalent female from a poorer habitat, small males may not be as effective at maintaining complete control over the female as either larger males in the aggregation, or as small males in lower quality habitats. Because high quality sites usually consist of dense aggregations of webs, it is easy for males to wander among webs. Although smaller residents have a prior residency advantage, it can be overcome if either the roving male is significantly ( $> 10\%$ ) larger, or if the resident is already engaged in a contest. In both cases the roving male is free to court and copulate with the resident female.

In the poorer quality areas small residents rare-

**Table 1.** Expected reproductive success for different sized males in high and low quality habitats

Male size (mm)	% mating	Poor habitat $\bar{x}$ no. females/males	Expected reproductive success	% mating	Good habitat $\bar{x}$ no. females/males	Expected reproductive success	
						Sperm competition	No sperm competition
1.5-1.7	0.60	1	24	0.0	0	0	0
1.8-2.0	0.86	1	28	0.25	1	15	15
2.1-2.3	1.0	1	112	0.40	1	45	45
2.4-2.6	1.0	1	145	0.72	1.6	120	167
2.7-2.9	0.0	0	0	1.0	3.0	420	630

ly incur these costs. Female density is low (Fig. 2), and rarely do wandering males locate the dispersed webs in these areas. Web occupants have a residency advantage and since wanderers are generally the smallest males, the likelihood of a small resident being displaced in the low quality habitats is significantly lower than in the high quality areas. This is clearly seen by following the fates of 204 marked males visiting the 27 focal webs (Table 1). Only in low quality areas are small males (1.5-1.7 mm) likely to find a web, displace the resident if one exists, and hold on to the web until mating occurs. And even in such habitats 40% of the males fail during some stage of the sequence.

Consequently, large resident males in good areas are potentially able to mate with more than one female, whereas smaller males in either good or poor areas are at best confined to a monogamous existence. Figure 9 shows the extent to which this polygyny potential is realized. Only males with cephalothoraces wider than 2.3 mm mate multiply.

Table 1 compares the size related reproductive potentials of males residing in high and low quality areas. Estimates of expected male reproductive success were derived by first using the assortative mating relationship (Fig. 7) to determine the size of the female that any male was likely to mate. Then the female body size-egg load relationship (Fig. 8) was used to estimate the number of eggs any sized male was likely to fertilize.

During this study 41 copulations were observed involving marked females who were monitored for many days before and after mating. Only 5 were seen to copulate twice, but clearly some sperm competition can occur (Jackson 1980; Vollrath 1980; Austad 1982). As a result two estimates of reproductive success were derived from mating success. One assumes complete sperm mixing when a male mates with a female in another male's web (Table 1, column 7), the other assumes complete sperm precedence by the male observed mating (Table 1, column 8). For males with cephalothoraces less wide than 2.3 mm expected reproductive

success is greatest in the lower quality sites, primarily because the likelihood of actually mating is highest. Although the likelihood of mating remains low in the good habitats even for moderate sized males (2.4-2.6 mm), the expected gain in the high and low quality areas are approximately equal. This parity arises because even moderately sized males that retain their position in an aggregation long enough to mate once have about a 45% chance of mating again (Fig. 9). For the largest males (>2.6 mm) the best strategy appears to dominate aggregations in high quality areas and mate as often as possible.

Thus only for middle sized males are there viable alternatives: small individuals fare better in the poorer quality sites, whereas the largest individuals fare best in the highest quality sites. Moderate sized spiders can obtain almost equivalent reproductive gains by tending females in the lower quality areas and receiving average benefits with virtual certainty. Or they can attempt to obtain a reproductive bonanza in the aggregations which form in the high quality areas. Since their chances of success are low in these sites choosing this strategy produces a high variance. On average, however, it yields the same expected reproductive benefits as the alternative.

## Discussion

### *Risk sensitive behavior*

In the spider *M. segmentata* male mating tactics are controlled by the distribution and behavior of females. Females aggregate in the best foraging areas and thus provide some males with enhanced reproductive opportunities. For large males the likelihood of gaining access to many females is great; for small males the likelihood is low. With small variances attached to these expectations it is predictable that small males should avoid high quality sites while the large males should restrict their movements to these places. For males at the

extremes of the size distribution, their behavioral options are clearly constrained, or conditioned (sensu Dawkins 1980), by relative body size.

For males in the middle of the range the situation is more complicated. Pursuing either the monogamous strategy in low quality areas, or the polygynous strategy in high quality areas yields on average equivalent reproductive rewards. The variances about these expectations, however, are quite different. Virtually all similarly sized males tending females in poor areas will mate and sire about the same number of offspring. For those attempting to defend females in aggregations, however, most will be cannibalized or be forced to emigrate. Only a few will obtain such disproportionate reproductive success. When faced with equal expectations, individuals that adopt tactics with high variances are behaving in a risk-prone fashion, whereas those adopting low variance tactics are behaving in a risk-averting manner (Caraco 1981; Real 1981; Rubenstein 1982). Figure 9 shows that among the 21 moderate sized (2.4–2.6 mm) males, 18 attempt to defend females in the high risk, high gain aggregations even though 28% fail to obtain any matings and only 33% mate more than once. With respect to mating behavior male *M. segmentata* are risk-prone.

Theory predicts that when investment in an activity results in decreasing returns animals should try to minimize the effects of uncertainty and thus behave in a risk-averting manner (Caraco 1981; Real 1981; Rubenstein 1982). In the context of foraging this is often the case. When faced with an uncertain environment animals diversify behavior (e.g. bumblebees, Oster and Heinrich 1976) or store resources (e.g. zooplankton, Lee 1975) in attempting to reduce uncertainty. And for those in good bodily condition, where energetic reserves are high, animals often behave conservatively. By minimizing the probability of catching too few prey they avoid jeopardizing their chances of surviving to reproduce (e.g. spiders, Gillespie and Caraco 1987).

Theory also predicts that when investment leads to increasing returns then selection should favor risk-prone behavior that maximizes the likelihood of obtaining the largest rewards (Caraco 1981; Real 1981; Rubenstein 1982). In foraging situations few animals probably experience situations where investment leads to increasing returns. One example, however, involves spiders having difficulty meeting their minimum daily energy requirement. For these individuals, Gillespie and Caraco (1987) show that they seek areas that sometimes offer very low, but at other times offer very

high prey availabilities. But perhaps the most frequent context in which investment leads to increasing returns involves male reproduction. Since male reproductive success is determined by maximizing numbers of matings, a seemingly small additional investment in searching or competitive behavior, could propel a male from not mating at all, to obtaining access to all the available females. When faced with alternative tactics yielding approximately equal reproductive success, *M. segmentata* males appear to behave in a risk-prone manner choosing to tend females in aggregations, the strategy offering the highest variance.

#### *Female alternatives*

From a female's perspective, habitat differences in prey availability will directly affect reproductive success. That females move their webs in search of areas providing large numbers of prey has been shown for *Archaeranea tepidariorum* (Turnbull 1964), *Argiope aurantia* (Enders 1977) and *Amaurobius similis* (Gillespie 1981). Even 13 fold increases in reproductive success (Riechert and Tracy 1975) can occur if females discriminate and move among sites. Female *M. segmentata* also move about and appear to respond to habitat differences in prey quality. But as Riechert (1976) has shown for *Agelenopsis aperta*, choosing sites that increase the period of feeding activity is also important. For *Agelenopsis* females, thermal stress, reduced time available for feeding, but for *M. segmentata*, lost feeding opportunities are associated with rebuilding webs destroyed by wind and rain.

Although *Meta* females move in response to changes in prey abundance the ability to aggregate appears to be constrained by features of the habitat, or competition from other females. Aggregations of individual webs of 'solitary' species have been noted in many other spiders (e.g. *Philoponella owenii*, Smith 1982; *Metepeira spinipes*, Uetz and Burgess 1979; *Cyrtophora moluccensis*, Lubin 1974; and *Nephila clavipes*, Farr 1977), and also only occur in areas of high prey availability. As Uetz et al. (1982) show, the aggregative tendencies of well nourished females is exactly the risk-averting behavior expected of females with energy reserves and experiencing diminishing returns on investment. But it may also be the case that by virtue of their size certain females are able to reduce their chances of being preyed upon by competing for central locations, even if some foraging costs are incurred. Such a trade-off has been shown for *Cyrtophora citricola* (Rypstra 1979), and may apply to other facultatively aggregating species (e.g.

Christenson 1984). For females, reproductive options appear to be determined in a clear-cut fashion. Both habitat quality, as well as relative size, determine where a female can construct her web.

#### *Problems of assessment*

The results of this study suggest that males and females assess site quality and the fighting potential of their opponents. For females establishing webs in vacant sites, the prey addition/removal experiments show that the rate of prey acquisition determines whether or not females remain or emigrate. Prey manipulation experiments on other spider species have yielded similar results (Turnbull 1964; Gillespie 1981; Riechert and Luczak 1982).

Usually understanding how spiders assess the quality of existing webs that they are attempting to take over is difficult. At least for *M. segmentata*, by comparing competing pairs of equal sized females in high and low quality areas it appears that contest lengths increase as resource value rises. This suggests that one, or both, of the contestants can assess the quality of occupied webs in different habitats. More work is needed, however, before it will be known whether the owner is responsible for the assessment as is the case for *Agelenopsis* spiders (Riechert 1982).

In *M. segmentata* assessment of fighting ability is based on body size. By gluing small metallic weights to the backs of females it was possible to reverse natural asymmetries among residents or wanderers. Over 85% of the size reversal trials were won by animals that would naturally have been more than 10% smaller. That size is such a good predictor of fighting ability in *M. segmentata* as well as other spiders (e.g. *Agelenopsis*, Riechert 1982), suggests that features of the web, such as resonancy, make information gathering accurate.

#### *Fitness balancing*

For *M. segmentata* alternative reproductive tactics are condition dependent. And although in such situations the reproductive gains of the alternatives are not expected to balance, they do so for moderately sized males. Since smaller males would fail too frequently in the aggregations, and larger males would forego too many opportunities by mating monogamously in the low quality habitats, moderately sized males appear to lie at a 'switch' point. Accurate assessments of fighting ability

most likely provide the means by which moderately sized males determine when it is profitable to change tactics. The mating behavior of *M. segmentata* underscores the fact that conditioned strategies need not be limited to situations in which animals are making the best of a bad situation, or that fitness balancing is limited to situations where the fitness of a tactic varies inversely with frequency.

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