Age-related sequential web building in the colonial spider Metepeira incrassata (Araneidae): an adaptive spacing strategy

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Colonial orb-weaving spiders provide insight into the proximate mechanisms by which social animals space themselves within a group. We examined mechanisms for the temporal patterns of web building that determine individual positions in Metepeira incrassata (Araneidae) colonies. The spiders display a characteristic age-related sequence of daily web building, with larger spiders completing their webs significantly earlier than smaller ones. We used data on behavioural interactions, web building, prey capture and predator attacks to evaluate four hypotheses. (1) Larger spiders are better competitors and pre-empt optimal spatial positions. (2) Smaller spiders reduce competition with larger individuals by building webs later. (3) Prey captured by different size classes is available at different times. (4) Differential predation risk determines web-building times. Large individuals dominated behavioural interactions. Disturbances by larger spiders during web construction significantly delayed the completion of smaller individuals’ webs and precipitated movements to new web sites. One prediction of the first hypothesis, that spatial needs translate into earlier building, was confirmed by significantly earlier web building by mature females with egg sacs (which are unable to move their egg sacs) compared with same-sized females without eggs (which can change locations freely). Experiments to determine whether the presence of large spiders inhibited the web building of smaller individuals were equivocal. Prey availability and risk of predation are not factors affecting web-building patterns. Sequential web building appears to be a result of both larger spiders competing to pre-empt space from one another and smaller individuals attempting to reduce conflict during web construction. Sequential web building is a proximate mechanism that influences spacing among colonial orb-weaving spiders and helps shape the typical hierarchical size distribution of spiders within the colony. Similar spacing mechanisms may be seen in colonial birds and marine invertebrates.
demographic spatial distribution: larger, more mature spiders are concentrated in the core of the colony with increasing numbers of progressively smaller individuals found towards the periphery (Rayor & Uetz 1990). Each individual builds and defends its own orb web that is connected to other webs by semipermanent framelines. The orb webs serve as temporarily fixed, multipurpose territories from which the spiders forage, breed, attach egg sacs, interact with neighbours and experience risks of predation (Uetz & Hieber 1997). Orb webs are rebuilt daily, typically in the same location for days to weeks (unpublished data). However, the selective pressures associated with web site location change as the spider matures: large spiders on the periphery of a colony are at significantly greater risk of predation than either members of their cohort in the core of the colony or smaller individuals on the periphery (Rayor & Uetz 1990, 1993; Rayor 1996). Smaller individuals forage more successfully on the periphery, and are at lower risk overall from predators (Rayor & Uetz 1993; Rayor 1996). The spatial structure of colonies is dynamic and thus influenced by mechanisms that operate over time as spiders change locations within the colony. When searching for a new site to build its web, a spider has three options: (1) aggressively take over another spider’s web or web site; (2) move to relatively unoccupied space on the peripheral framelines of the colony; or (3) build between other established webs. Within M. incrassata colonies, all three occur, but their success is not equally probable. To displace an established spider successfully and take over its web site, the aggressor typically must be larger than the resident (Uetz & Hodge 1990; Hodge & Uetz 1995). Web take-overs are not sufficiently frequent to account for the observed flux within the colony for spiders of all sizes (Uetz & Hodge 1990; Rayor & Uetz 1993). Nor is colony growth due to the addition of new spiders to the periphery of established webs (Rayor & Uetz 1990). Building between established webs is the most probable option, similar to the settlement patterns proposed by Getty (1981). Thus, to understand group spatial organization, it is necessary to examine these underlying proximate mechanisms.

Preliminary observations suggest that a differential pattern of web building in the morning, in which larger spiders complete web construction earlier and smaller spiders later, is responsible for the spatial and demographic structure of the spider colony. This temporal pattern of age-related sequential web building has the potential to determine the location within the colony where individuals could construct their webs and to reveal what factors cause individuals to move to new locations. We generated a null hypothesis and several (nonexclusive) alternative hypotheses to explain the pattern of sequential web building.

(1) The timing of orb web completion is independent of spider size (null hypothesis).

(2) Larger spiders are superior competitors that build earlier to pre-empt space for their large webs. Three predictions arise from this hypothesis. (a) Larger spiders win more disputes over webs. (b) Larger spiders will have larger webs that require more space. (c) Because large spiders that build later in the day may not have sufficient space to construct a web without conflicts, spiders whose web sites are fixed (i.e. females guarding egg sacs), will build earlier than spiders of the same size that are free to move to alternative sites.

(3) Smaller spiders reduce competition with larger individuals by building webs later. Predictions: (a) smaller individuals building webs earlier experience more aggression than individuals starting later; (b) in the absence of larger spiders, smaller spiders will build webs earlier.

(4) As spiders need finished webs to capture prey, and spider size limits the size of prey that can be captured successfully, the spiders time web completion to match the availability of appropriately sized prey. Predictions: (a) availability of prey of different sizes will vary with time of day; (b) large prey will be caught more often early in the morning, while small prey will be caught in mid-to late morning.

(5) Differential predation risk causes size classes at greater risk to shift web-building times away from periods of predator activity. Prediction: predator activity will vary with time of day.

To determine which of these hypotheses best explains possible proximate mechanisms responsible for the spatial structure of M. incrassata colonies, we observed naturally occurring colonies and experimentally manipulated artificial colonies of specific size composition to determine the temporal sequence of web building relative to spider size.

**METHODS**

**Subjects and Study Area**

Colonial M. incrassata were studied in Fortin de las Flores, Veracruz, Mexico during November–December 1988 and October–November 1989. Spiders of two naturally occurring (Alicia, Cactus) and four artificially established colonies (Posada, Cage’88, Cage’89, M&S) were studied on the grounds of a hotel and a small coffee plantation. Study areas are described in detail in Rayor & Uetz (1990) and Uetz & Hodge (1990). Colonies were not enclosed: insect prey and spider predators could enter freely. Five of these colonies, designated ‘control colonies’, contained spiders of all age–sex classes, typical for M. incrassata colonies; one colony (M&S) was experimentally composed only of spiders of medium and small size classes. Control colonies contained 300–750 individuals; the M&S experimental colony contained approximately 125 individuals. We measured spider body lengths to the nearest millimetre, but for some analyses, grouped them into small (1–3 mm), medium (4–5 mm) and large (6–8 mm) categories using characteristic abdominal and cephalothoracic features. All ‘large’ individuals were assumed to be reproductively mature.

**Data Collection and Analysis**

We made two different measures of the relationship between spider size and the timing of web building. In
the first measure (web completion), we recorded the times at which spiders within a colony completed their webs to determine the sequence of web building among spiders of different size classes. In the second measure (web construction), we observed individual spiders from start to completion of their webs to determine the time required to construct webs for spiders of different size classes.

To measure web completion, we simultaneously observed as many spiders as possible within a single colony (range 69–160 individuals) from the first construction activity near dawn until the last few spiders completed their webs at approximately 1130 hours. We recorded the time at which each spider completed its web, the spider’s size, its web diameter and its location within the colony (core or periphery). For each mature female, we recorded the presence or absence of egg sacs. We measured web completion on 9 days from the five control colonies. We considered data collected on different dates from a given colony to be independent measures due to the long time intervals between measures (20–57 days), and because the number of spiders in the colonies was much greater than the number from which data were collected. To analyse the sequence of web building and the relationship between spider size and web size, we evaluated the data using a SAS general linear model (GLM) with a random effects two-way analysis of variance (ANOVA), in which time or web size were the response variables, spider size class and location were fixed treatment factors and individuals were replicates. We used similar GLM two-way ANOVAs to analyse all web completion and construction data unless indicated otherwise. Tests of residuals indicated homoscedasticity for all data sets, validating assumptions of the GLM ANOVAs.

To compare the time when mature females with and without egg sacs completed their webs, we pooled web completion data from each of the five colonies. Because eggs take approximately 4 weeks to develop, we used only a single date per colony to minimize the possibility of overlapping measures of the same females.

To measure web construction, we monitored randomly selected individuals of all size classes (N=144) before morning activity began until webs were completed. We recorded the web diameter and total time taken to build webs for members of each size class, along with the number of individuals that changed web sites or were disrupted. We collected data on 6 days from the Cactus and Posada colonies. Because web construction time recorded for each colony did not differ between dates and there were no significant differences between the colonies (ANOVA: $F_{1,72} = 0.57$, NS), we combined dates for statistical analysis. We evaluated web-building effort as the amount of time (in minutes) taken to construct each cm$^2$ of orb web.

To determine experimentally the influence of the presence of larger spiders on the time taken by smaller individuals to complete their webs, we established an experimental colony (M&S) composed of only medium and small spiders near the control colonies, Posada and Cactus, 1 week prior to the first comparison. All three colonies were located 2–4 m from one another in similar habitat (ornamental bushes and cactuses surrounded by mowed lawn) and received equal exposure to the sun. On three different days, we simultaneously recorded web completion times from spiders in experimental (M&S) and control colonies (Posada, twice; Cactus, once). We analysed the data using a SAS GLM one-way ANOVA using contrast measures between time of web completion in control and experimental colonies (factors) for the small and medium size classes in each colony, and for all size classes averaged together.

We assessed the outcome of 275 dyadic agonistic interactions over web sites by the relative size of the individual’s opponent (larger, equal, smaller), and by the frequency with which that resident or intruder won agonistic interactions against opponents of various sizes.

We determined the timing of prey captures for spiders of different size classes by analysis of data from direct observations of prey capture (N=1350 prey) in multiple colonies during 1987–1989. (Details of prey capture measures are in Uetz 1989; Rayor & Uetz 1990, 1993; Uetz & Hodge 1990.) To determine whether prey of various sizes were differentially available at different times of the morning, we performed a one-way ANOVA on log-transformed prey size data by time periods. We assessed the relationship between time of day and the size of prey captured by spiders of different sizes by using a three-way G test of the null hypothesis of independence.

**RESULTS AND DISCUSSION**

**Spider Size and Web Construction**

There was a characteristic order in which spiders of different sizes built their webs (Fig. 1). In all colonies (N=8), larger spiders completed web building.
significantly earlier than did smaller individuals (ANOVA: all \( F_{1,54\&1,127}=15.5 \leq 88.9 \), all \( P<0.0001 \)). For each size class, there was no significant difference in the time at which webs were completed between the core and periphery. Only in one colony (Alicia), was there an interaction between the size of the spider and its location relative to the time when the webs were completed (\( F_{2,129}=4.65, P=0.033 \)), with large spiders in the core building earlier than large spiders on the periphery. The null hypothesis of independence between spider size and web completion time can therefore be rejected.

There was a highly significant colony effect on the web completion time (two-way ANOVA: \( F_{8,98}=7.95, P<0.0001 \)), although the actual patterns observed were the same in all colonies. Within a colony, there was an effect of date on the time that webs were completed. Therefore, we analysed data from each colony on different dates independently. Variation among colonies and dates within colonies was related to the relative slopes or speed with which web building in different size classes occurred relative to the time when webs were started (as in Fig. 1). On cool days, when web building was initiated later in the morning (0900 hours), spiders of all size classes initiated and completed their web construction more quickly (resulting in a steeper regression slope) than on warmer days, when web building was initiated earlier (0600 hours).

### Alternative Hypotheses: Proximate Mechanisms

Hypotheses concerning mechanisms responsible for the observed sequential web-building pattern and the characteristic spatial organization of *M. incrassata* colonies can be separated into those that suggest a basis in competitive interactions between individuals (hypotheses 1 and 2), versus those suggesting that non-competitive factors, such as differential prey availability (hypothesis 3) or predation risk (hypothesis 4), cause shifts in the temporal patterns of web building. For each hypothesis, we examined the assumption that optimal web space, a position that allows foraging success with minimal intraspecific conflict and risk of predation, is at a premium within the colony.

**Large Spiders Are Superior Competitors and Pre-empt Space**

Larger spiders consistently won agonistic interactions with medium or small individuals, while medium spiders won over smaller individuals (Table 1). Larger spiders had encounters with smaller individuals 73% of the time, and won these encounters 100% of the time when they were the resident and 71% when they were the intruder. Similarly, while medium-sized residents only won 26.7% of the agonistic interactions against large intruders, medium-sized intruders were often successful against smaller residents (51%). In contrast, 80% of small spiders’ agonistic encounters were with larger individuals and small web residents rarely (5%) won agonistic interactions against intruders. This evidence supports both the hypothesis that large spiders are better competitors that win more disputes and that smaller spiders should attempt to minimize conflicts with larger individuals.

Because the size of orb webs increase with spider size, large spiders require more space for their webs (Fig. 2a): two-way ANOVA: all \( F \) values \( 1.76 \leq 1.127 \leq 10.25 \leq 58.83 \), all \( P<0.0001 \); colony: \( N=7 \), \( R^2=0.513–0.799 \). As expected, construction time increased with web size (Fig. 2b). The size of the webs and the time taken to construct webs did not differ significantly between individuals of similar size on the core and the periphery. Construction time was more closely associated with web size than with spider size, as has been reported in other studies on orb webs (Leborgne & Pasquet 1987; Sherman 1994) and may be due to the relative effort involved in web construction for spiders of different size classes. The amount of effort required, assessed as the construction time per cm² of orb web (Fig. 3), was much greater for smaller spiders than for larger individuals in both colonies (Spearman rank correlation: Cactus: \( r_s=0.81, N=8, P<0.02 \); Posada: \( r_s=0.93, N=7, P<0.01 \)). These data further support hypothesis 1 in

### Table 1. The relative size of the opponents for each size class and the percentage of residents and intruders that won agonistic interactions (\( N=275 \) dyadic interactions)

<table>
<thead>
<tr>
<th>Spider size class</th>
<th>Relative size of opponent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Larger</td>
</tr>
<tr>
<td><strong>Encounters (%)</strong></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>122</td>
</tr>
<tr>
<td>Medium</td>
<td>262</td>
</tr>
<tr>
<td>Large</td>
<td>167</td>
</tr>
<tr>
<td><strong>Wins as resident</strong></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>114</td>
</tr>
<tr>
<td>Medium</td>
<td>130</td>
</tr>
<tr>
<td>Large</td>
<td>131</td>
</tr>
<tr>
<td><strong>Wins as intruder</strong></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>78</td>
</tr>
<tr>
<td>Medium</td>
<td>187</td>
</tr>
<tr>
<td>Large</td>
<td>58</td>
</tr>
</tbody>
</table>

For each size class we compared the frequency of winning against spiders that were larger, equal in size, or smaller than their opponents. Because we calculated the outcome for each member of the dyadic interaction, the sample size of 275 is doubled for each measure.
that larger spiders construct larger webs that require more space than those of smaller individuals.

Another prediction of hypothesis 1 is that large spiders building later in the day may not have sufficient space to construct their web without conflict. It follows that individuals constrained to a fixed location should pre-empt that space by building earlier than individuals capable of relocating. A natural test of this prediction is whether females with egg sacs build earlier than mature females of similar size without egg sacs (6–8 mm). Egg sacs are fixed above a female’s orb, on a line attached to the hub, and guarded for 4–6 weeks. Unguarded egg sacs are parasitized significantly more often (Rayor & Uetz 1990). Thus, females guarding egg sacs are constrained to build their daily orb web in a fixed location. Reproductively mature females with egg sacs completed webs significantly earlier than the same-sized mature females without eggs (5 colonies: \( X = 45.42 \) min earlier, range 35.0–61.4 min). In pooled data from five colonies combined, 106 mature females with eggs completed webs at 0737 hours ± 24.6 min, while 148 mature females without eggs completed webs at 0822 hours ± 47.7 min (ANOVA: \( F_{1,227} = 38.3, P < 0.001 \)).

Taken together, these diverse data support our first hypothesis, that larger spiders are superior competitors that pre-empt optimal spatial positions within the colony. Because the colony core is much safer for larger spiders it is optimal (Rayor & Uetz 1990, 1993), but because space in the core is limited, earlier web building serves to pre-empt the needed space from other large individuals. Competitive interactions over space among large spiders and behavioural dominance over smaller individuals characterizes the web-building behaviour of large individuals.

**Smaller Spiders Avoid Competition By Building Later**

Smaller individuals are more likely to evoke threats from larger spiders if they start to build their webs while larger spiders are still building (as in *Cyrtophora moluccensis*, Lubin 1974), but less likely once larger spiders have settled onto completed webs. During 20.8% (30/144) of focal observations of web building, smaller spiders were disturbed, often repeatedly, by vibrations from the web-building activity of larger spiders or by aggressive vibratory threat plucks from larger individuals. The disturbed individual responded by immediately ceasing web construction, returning to the hub, and pulling its legs close to its body for some period of time (see also Hodge & Uetz 1995). Spiders that were disturbed by conflicts with larger spiders during web construction took significantly longer to complete their webs than undisturbed spiders of the same size class (Mann-Whitney test: small: \( Z = 2.6, N_d = 3, N_u = 28, P = 0.0039 \); medium: \( Z = 6.0, N_d = 19, N_u = 36, P < 0.0001 \); large: \( Z = 2.5, N_d = 4, N_u = 38, P < 0.0048 \); Fig. 4). Of the 30 individuals that were observed to be disturbed while building, four (13.3%) abandoned the web site and relocated elsewhere. Of the 144 individuals...
observed, 11 (7.6%) moved prior to web construction to a different web site from the one they had occupied overnight without an apparent source of disturbance to precipitate the move. Smaller individuals benefit by avoiding direct competition with bigger animals, because larger individuals virtually always win (Table 1). These results support predictions of hypothesis 2 that smaller spiders reduce competition with larger individuals by building webs later.

To determine whether the presence of large spiders was a causal mechanism underlying later web building by smaller spiders on three dates, we simultaneously compared the time webs were completed between an experimental colony (M&S) containing only medium and small spiders and a control colony containing all spider size classes (Posada, two dates: Posada 1, Posada 2; Cactus, once). In two separate trials, spiders in the experimental colony finished building webs significantly earlier than similar-sized individuals in the Posada colony (Fig. 5, Table 2). In a third trial, small and medium individuals from both the experimental and the control colony built at the same time (Fig. 5, Table 2). In the experimental colony, differences in the time that spiders of different sizes completed webs remained significant (N=3, all \( P<0.0001 \)).

Jakob et al. (1998) examined whether large spiders inhibited web building by smaller individuals and found no significant differences in the times of web building in colonies with and without large individuals. They compared web-building times between small numbers of recently caged spiders in single age class groups and those in a cage of mixed age classes. It is not apparent why spiders in the Posada colony were more affected by the presence of large individuals than those in the Cactus colony, or than those in the colonies studied by Jakob et al. Possibilities include features particular to individual colonies, such as relative density or the period of experience without the presence of larger individuals. For example, because the Cactus colony had relatively few large spiders on the periphery, the activities of the larger spiders in the core may not have directly affected the more distant peripheral individuals. In contrast, the Posada colony had a more spatially integrated mix of all age classes and the activities of the larger spiders were generally more disruptive. Clearly, larger spiders have the potential to inhibit the web-building behaviour of smaller individuals, but are unlikely to be the sole factor controlling the sequence of web building.

Even if disruption by larger individuals is a major force affecting the sequence of web building in colonies, there is likely to be some circadian rhythm associated with web

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**Figure 4.** Mean±SE web construction time of undisturbed (□) spiders and spiders that were disturbed or interrupted (■) during web construction. Disturbed spiders took significantly longer than undisturbed spiders to build webs (Mann–Whitney \( U \), all \( P<0.004 \)). Sample sizes are inset in bars.

**Figure 5.** Mean±SE time of day that webs were completed for each size class of spiders in control colonies (Posada 1: □; Posada 2: ○; Cactus: △), with all size classes compared to the time of day that webs were simultaneously completed by small and medium spiders in the experimental colony M&S (□, ○, and △) on the same days.

**Table 2.** The results of ANOVA comparing mean web completion time in control (Posada 1, Posada 2, Cactus 1) and experimental (M&S) colonies for small- and medium-sized spiders and for control versus experimental colonies overall.

<table>
<thead>
<tr>
<th></th>
<th>Experimental vs. control</th>
<th>Posada 1</th>
<th>Posada 2</th>
<th>Cactus</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Size classes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td></td>
<td>35.0</td>
<td>40.9</td>
<td>0.0</td>
</tr>
<tr>
<td>( F )</td>
<td></td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.98</td>
</tr>
<tr>
<td>( N )</td>
<td></td>
<td>53</td>
<td>53</td>
<td>21</td>
</tr>
<tr>
<td>( N )</td>
<td></td>
<td>54</td>
<td>53</td>
<td>29</td>
</tr>
<tr>
<td>Medium</td>
<td></td>
<td>23.2</td>
<td>34.3</td>
<td>0.46</td>
</tr>
<tr>
<td>( F )</td>
<td></td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.50</td>
</tr>
<tr>
<td>( N )</td>
<td></td>
<td>37</td>
<td>39</td>
<td>21</td>
</tr>
<tr>
<td>( N )</td>
<td></td>
<td>25</td>
<td>40</td>
<td>43</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>57.8</td>
<td>71.8</td>
<td>0.09</td>
</tr>
<tr>
<td>( F )</td>
<td></td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.76</td>
</tr>
<tr>
<td>( N )</td>
<td></td>
<td>50</td>
<td>53</td>
<td>48</td>
</tr>
</tbody>
</table>

Contrast equations were compared using SAS GLM procedure (see text for details).
Differential Predation

Although differential predation could be responsible for shifting web building away from periods of high predator activity, it is unlikely to be responsible for the observed sequential web building. Few diurnal invertebrate predators (pompilid and sphecid wasps) or parasitoids (sarcophagid flies, ichneumonid wasps) attacked prior to 1000 hours; 96.7% (N=4/122) of all invertebrate attack bouts (a bout is a group of attacks that occur sequentially in a discrete time period) occurred between 1000 and 1500 hours. Yet large and medium spiders consistently completed webs well before 1000 hours, with only the small spiders occasionally completing webs after that time. The exceptions to the disjunction between predator activity and web-building activities were: (1) all attack bouts (N=4) by hummingbirds occurred between 0700-0800 hours; (2) two of the 58 attack bouts by predatory wasps (Poecilopompilus mixtus: Pompilidae and an unidentified sphecid) occurred prior to 1000 hours (see Rayor 1996 for further details); and (3) two of the 52 attack bouts by the parasitoid fly (Arachniomyia lindae: Sarcophagidae) occurred before 1000 hours. The spiders were more vulnerable to predation when distracted by other activities (Rayor 1996), but were never observed to be attacked while constructing webs.

Conclusions

Our evaluation of several hypotheses suggests that a combination of factors cause the observed temporal pattern of sequential web building seen in M. incrassata colonies. Large spiders compete with one another to pre-empt prime web space within the colony. Spiders behaviourally dominate individuals smaller than themselves, causing smaller individuals to delay web building to reduce conflict. The consequence of these two interacting factors is the observed temporal pattern of aged-related, sequential web building. A consequence of sequential web building is that smaller individuals are gradually pushed away from larger spiders in the core of the colony and towards the periphery, resulting in the observed spatial structure of the colony. Sequential web building thus appears to be the proximate mechanism responsible for the previously reported adaptive spacing strategy in colonial spiders (Rayor & Uetz 1990, 1993). Instead of spiders fighting for optimal positions within the colony on a daily basis, the spiders use the less aggressive method of adult pre-emptive web building as a more subtle form of competition for space within the colony.

Prey Availability

Because the sticky spiral is the last element of the orb constructed, insect prey can only be captured after the spider has begun this final spiral. Hypothesis 3 predicted that web completion time should match the availability of appropriately sized prey. We estimated differences in cumulative prey capture during the period of web construction (0830–1130 hours) using hourly measures of prey capture rates and a weighted mean of web completion time for each size class.

These results do not support the prediction that spiders time the completion of their web to match the availability of appropriately sized prey. However, the earlier any spider completes its web, the greater its cumulative prey capture. Spiders that are disrupted and delay web completion are likely to incur considerable costs as they capture fewer prey items during the day. Multiple days with poor prey capture could slow the developmental rate of young spiders (Vollrath 1985; Uetz 1992; Higgins 1995) and induce the individual to move to a position within the colony where conflicts during web construction were decreased.

Figure 6. Estimated cumulative daily prey capture for spiders of different size classes (small, medium, large). Data were collected using hourly measures of prey capture rates and a weighted mean of web completion time for each size class.
The web-building patterns seen in *M. incrassata* are found in both solitary and colonial orb-weaving spiders. Web size increases with spider size and, not surprisingly, larger webs take longer to build (e.g. Higgins & Buskirk 1992; Sherman 1994). In aggregations of spiders, young spiders commonly intercalate their webs among those of adults, and move elsewhere as their webs get larger (Lubin 1974; Smith 1982). A size-dependent temporal sequence of web building is seen in some other dense aggregations of spiders (Kremer et al. 1987; Leborgne & Pasquet 1987; Ward & Lubin 1992). In a restricted space, the first orb weaver to build her web has a significantly larger web than the second spider, indicating the importance of pre-emption (Leborgne & Pasquet 1987). In dense inter- and intraspecific groups of orb weavers, Ward & Lubin (1992) observed a reversed sequence of web building, where nocturnally active small spiders build earlier and larger spiders build later. Unlike our results, Ward & Lubin concluded that the timing of web building correlated with prey size, which increased as the night progressed.

Age-related sequential web building has not been reported in most other colonial orb-weaving species, perhaps because the spiders are in groups of the same size class (e.g. *Parawixia bistriata*; Fowler & Diehl 1978), because the orbs are not rebuilt daily (e.g. *Cyrtophora* sp., Lubin 1974; *Philoponella* sp., Smith 1982), or most likely because sequential building has not been looked for. Thus far, sequential web building in colonial spiders has only been reported for *Metabus gravidus* (Araneidae), which builds groups of horizontal orb webs over streams in cloudforests in Costa Rica (Buskirk 1975a,b). Larger *M. gravidus* are found over the centre of the stream and smaller individuals are found closer to the bank (Buskirk 1975a). Buskirk’s (1975a) observations on web-building patterns in *Metabus* are remarkably similar to those seen in *Metepeira* colonies: (1) larger spiders build earlier than juveniles; (2) the larger the spider, the more time it spends on the prey capture web; (3) smaller spiders that start to build webs while larger spiders are building frequently have their webs torn down and must start over elsewhere; and (4) when few adults are present, juveniles build earlier in the morning and stay active longer. We predict that age-related, sequential web building will be found in other colonial spider species.

Some aspects of age-related sequential settlement observed to determine relative spatial positions within *M. incrassata* colonies are unique to web-building spiders. However, patterns of pre-emption of prime space within a group, whereby older animals compete with one another and younger animals avoid competition by moving to less desired space on the periphery of the group, is observed in a diverse array of colonial animals (birds, lizards, fish, marine invertebrates). For example, most colonies are typically settled first by larger or more mature individuals, with younger animals arriving later. Optimal positions, often in the safer core of the colony, are occupied first (Robinson 1986; Jones 1987; Dupuis & Keenleyside 1988; Kharitonov & Siegel-Causey 1988). Younger or smaller animals that attempt to settle in core positions early are aggressively displaced (Robinson 1986) and subsequently establish sites in peripheral and/or riskier positions. The extent of disruption during settlement (or courtship) has been proposed to determine relative spacing and density within groups (Foster 1983). Age- or size-related direct and indirect conflicts determine both the position within the group and the defensive strategies of the individuals (Kharitonov & Siegel-Causey 1988; Harvell & Padilla 1990; Harvell 1991). Although predator pressure appears to affect which sites within a group are optimal (i.e. Tenaza 1971; Robinson 1986), predation alone does not seem to be a major factor in determining settlement patterns within the group. Similarly, differential food availability typically does not appear to determine colony settlement, even for those animals that forage exclusively from their territories. Age-related sequential settlement determining colony structure may be a pattern general to many colonial organisms.

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