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THE EFFECT OF CONSPECIFICS ON THE TIMING OF ORB CONSTRUCTION IN A COLONIAL SPIDER

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ABSTRACT. *Metepeira incrassata* (F.O. Pickard-Cambridge 1903) (Araneae, Araneidae) are colonial spiders that share a common and relatively permanent framework of silk, but that construct and defend individual orbs within the communal framework. Orbs are taken down nightly and replaced in the morning. Larger spiders generally begin orb construction before smaller spiders do. We tested whether this pattern results from interactions among spiders of different size classes. We constructed artificial colonies that contained either a mixture of size classes or a single size class. In two replicates, spiders that were housed in single-size groups built their orbs at the same time as their counterparts in mixed groups. We suggest that conspecific interaction is unlikely to be the only factor determining the differences in the timing of orb construction among size classes in this species.

Metepeira incrassata are colonial spiders that live in large groups and share a common space web that is relatively permanent. Within this silk framework each spider constructs its own orb and defends it against intruders. Orbs are ingested by the owners at the end of the foraging day, and rebuilt again in the morning. Within a colony, spiders are typically segregated by size: larger spiders are generally found in the core, where predation risk and food level are low, and smaller ones are generally on the periphery, where predation risk and food level are higher (Rayor & Uetz 1990; Rayor & Uetz 1993). This colony structure may occur because the optimal location within a colony differs across size classes (Rayor & Uetz 1993), or because some spiders are excluded from favorable positions by conspecifics, or a combination of both. *M. incrassata* often fight over potential orb sites, and large spiders are likely to have the advantage: size has been shown to be a determinant of winning aggressive interactions in this species (Hodge & Uetz 1990, 1995), as in other spider species (e.g., Austad 1983; Buskirk 1975; Christenson & Goist 1979; Jakob 1991; Jakob 1994; Riechert 1978a; Riechert 1978b; Wells 1988). Large *M. incrassata* released into a colony of smaller individuals displaced smaller individuals from the core (Rayor & Uetz 1990).

Large spiders have a further advantage in web establishment because they build their orb webs earlier in the foraging period than do smaller spiders. Large spiders, followed by medium and small spiders, generally begin orb construction at first light. It is not clear if this temporal pattern in web construction occurs because of interactions between the size classes: small spiders may be inhibited by the presence of larger spiders and delay web construction, or perhaps large spiders begin web construction earlier when in the presence of smaller spiders in order to secure the best foraging sites. We tested this hypothesis by constructing small colonies with and without larger competitors, and noting the time that web building began and ended. We predicted that, if spiders are influenced by the presence of conspecifics, those in groups composed only of individuals of the same size would differ in the time of orb construction compared to spiders in mixed-size groups.

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METHODS

The study site was in Fortin de las Flores (19°N, 97°W, 1000 m elevation), in Veracruz, Mexico (for detailed description of study area, see Uetz & Hodge 1990). Six 1 m^3 cages were constructed of polyvinyl chloride ("PVC") pipe and covered with fine mesh. They were set on a patio that was open to the air but roofed so it was protected from rain. Pairs of cages were placed next to one another. The position of the cage pairs on the patio was decided randomly.

All spiders were collected from a nearby large colony, estimated to be several thousand individuals in size. In order to eliminate the need for experimental spiders to invest an unusually large amount of energy on the construction of communal space webs in the experimental cages, approximately 25 adults were introduced into each cage. After two days, these spiders were removed early in the morning prior to orb-web construction and were not used in the experiment.

For each of two replicates, we established three cages that each contained spiders of a single size class: either 15 large females (7–10 mm), 20 medium (4–6 mm), or 40 small (1–3 mm) spiders (medium and small spiders could not be sexed). Each cage of single-sized individuals was paired with a cage of mixed-size individuals that contained 15 large, 20 medium, and 40 small spiders. These numbers were chosen to reflect the typical composition of age classes and spider densities in the field. Spiders were released unmarked into the cages two days before the day of the test in order to be given time to acclimate. The two replicates were conducted five days apart.

We began watching spiders when they began to move during the hour prior to dawn. We recorded the behavior of each spider using the technique of scan sampling (Altmann 1974), in which behaviors of individuals in a group are noted in sequence. We examined each cage every 15 minutes in the same order each time. Pairs of cages were examined either simultaneously or in rapid sequence. Data collection stopped when all or nearly all webs were complete, generally around noon. For each spider, we noted on audiocassette its size, and whether it was laying down communal space web, the radii of its orb, a temporary spiral, a permanent spiral, or was sitting at the hub of a complete web (for a more detailed description of orb construction, see Foelix 1996; Uetz et al. 1994).

Because of the brevity of some of the stages in web-building relative to the 15 min interval between scans, we focused on two pieces of data: the time when permanent spirals were begun and when orbs were completed. Both measures together allowed us to examine the possibility that the presence of conspecifics does not affect the time of web initiation, but slows the process of web construction, perhaps through interruptions. We used an ANOVA design to examine simultaneously the three main effects: replicate, spider size class, and cage composition, as well as the interaction between size class and cage composition. A significant interaction would indicate that changes in the timing of web construction are influenced by group composition. The data did not fit the assumptions of standard ANOVA methods, so we used a nonparametric bootstrap analysis to obtain the null distributions of the *F*s, from which we calculated the significance levels in the ANOVA design. In parametric statistical approaches, the null distributions are obtained mathematically from sampling theory, under the assumptions of normally distributed residuals and homoscedasticity of variances, and reflect the variation that would be produced in the statistics under random sampling error alone. In a bootstrap analysis, the null distributions are obtained by repeatedly calculating the statistics of interest on random samples from the original data (Efron 1982; Efron & Tibshirani 1993). This creates distributions that vary only because of sampling error, without invoking the assumptions of standard mathematical approaches. Significance may then be assessed from these null distributions by the percentile method: observed values in the *n*th percentile reflect significance at the $P \leq 1/(2n)$ level (Efron 1982; Efron & Tibshirani 1993). Our calculations were made using a general linear model program for ANOVA written in THINK® Pascal v4.2 (Symantec Corp.) by AHP and run on a Macintosh PowerPC® 9500, and the calculation of the ANOVA table was checked using the statistical program SuperANOVA® v1.1 (Abacus). We used 1000 bootstrap replicates in our tests; so to be conservative, we report *P* values to only two decimal places.

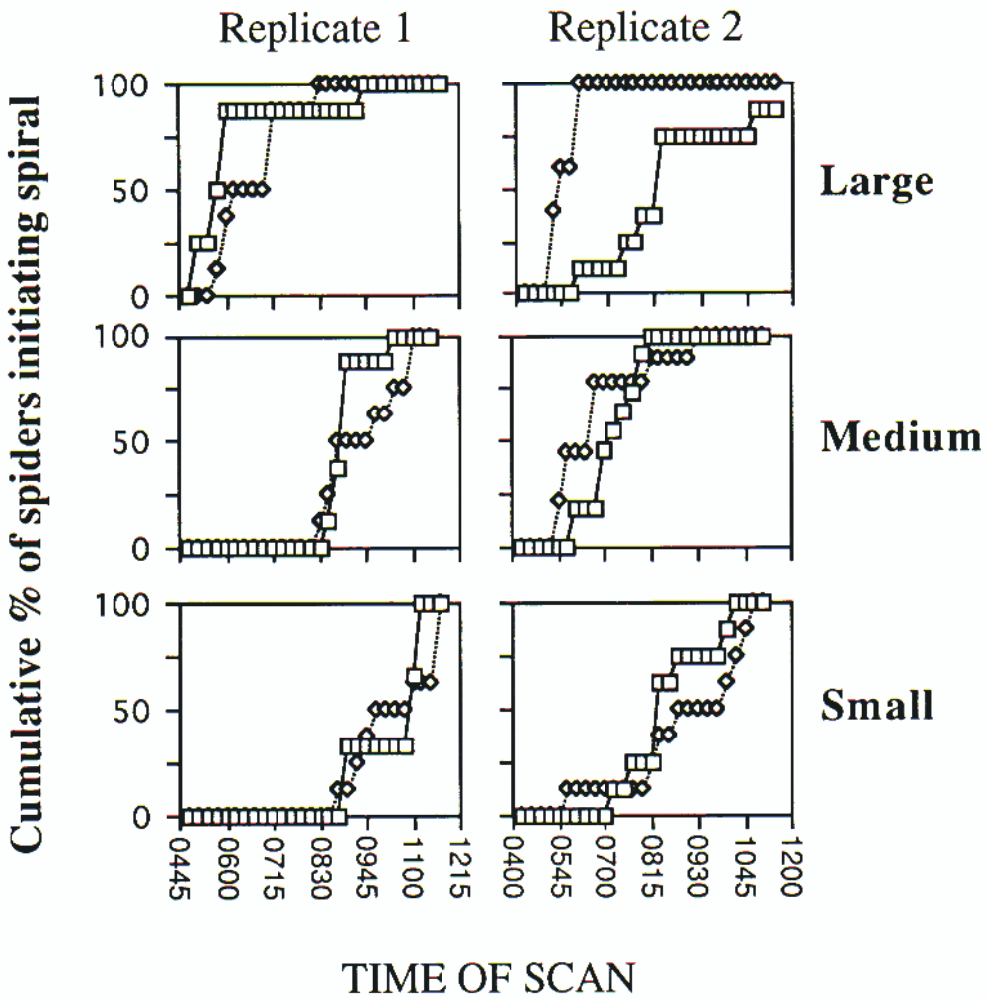

Figure 1.—Cumulative percentage of spiders that initiated the permanent spiral. Diamonds (◊) represent single-size class colonies and squares (□) represent mixed size-class colonies. The x-axis represents the starting times of scans taken at 15 minute intervals beginning at the onset of web-building activity.

Follow-up comparisons were done using Mann-Whitney *U*-tests for each trial.

Voucher specimens are deposited at the Museum of Comparative Zoology at Harvard.

RESULTS

Not all spiders built orbs in our experimental conditions, especially small spiders. Several molted during the course of the experiment, and spiders generally stop feeding just prior to a molt (Foelix 1996). There were no differences between the number of spiders that built webs in the different treatment types (contingency table, *G*-test, $P > 0.4$ in all cases; number of spiders that were active ranged from 60–92% of spiders per cage). There were highly significant differences between replicates in the timing of web-building (Tables 1 and 2, $P < 0.01$), which probably reflect daily variation in temperature and light level (mainly cloud cover) in the early morning hours.

We confirmed previous observations that large spiders build their webs earlier than did medium spiders, which in turn build their webs before small spiders (Figs. 1–3). This is reflected in the size-class main effects of Table 1 (initiation of permanent spiral, $P < 0.01$) and Table 2 (web completion, $P < 0.01$), where small, medium and large spiders are compared. In follow-up tests, all pair-wise comparisons between size classes were signif-

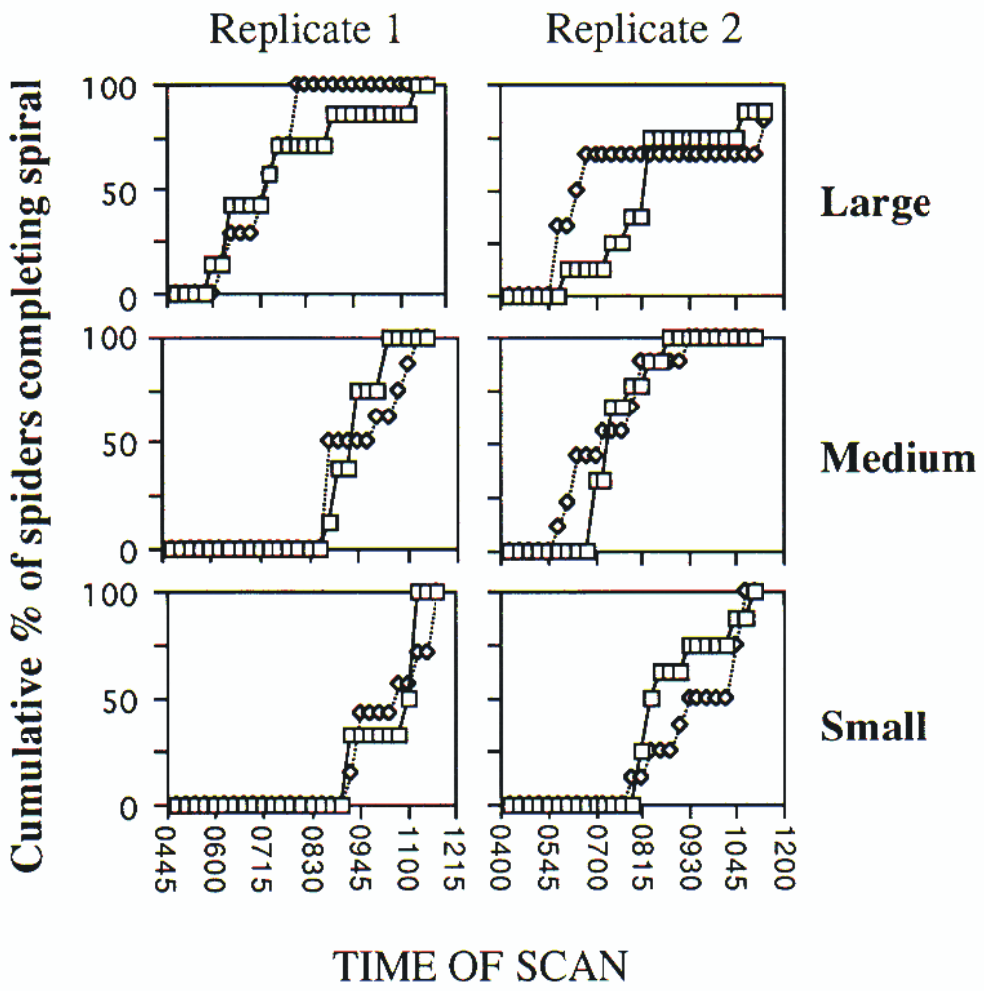

Figure 2.—Percentage of spiders with completed orbs. Diamonds (◇) indicate single-size class colonies and squares (□) indicate mixed size-class colonies. The x-axis represents the starting times of scans taken at 15 minute intervals beginning at the onset of web-building activity.

Table 1.—ANOVA on the time of initiation of the permanent spiral. *P*-values are derived from 1000 bootstrap replicates.

Source	*df*	Sum of squares	Mean squares	*F*	*P*
replicate	1	1130.301	1130.301	41.210	<0.01
size class	2	1733.343	866.671	31.598	<0.01
cage composition	1	55.811	55.811	2.035	0.15
size class × cage composition	2	76.216	38.108	1.389	0.23
residual	85	2331.388	27.428		
Total	91	5035.163			

Table 2.—ANOVA on the time of completion of the orb. *P*-values are derived from 1000 bootstrap replicates.

Source	*df*	Sum of squares	Mean squares	*F*	*P*
replicate	1	477.709	477.709	17.622	<0.01
size class	2	1281.573	640.787	23.638	<0.01
cage composition	1	10.489	10.489	0.387	0.55
size class × cage composition	2	75.359	37.680	1.390	0.26
residual	85	2222.860	27.108		
Total	91	3939.978			

icant in both replicates (Mann-Whitney *U*, $P < 0.02$ in all cases) with the exception of large vs. medium spiders in replicate 2, where the timing of spiral initiation and web completion did not significantly differ. There was no discernible effect of cage composition (single-size groups vs. mixed-size groups) on the timing of web building (Figs. 1, 2; Table 1, initiation of permanent spiral, $P = 0.15$; Table 2, web completion, $P = 0.55$).

We found no evidence that interactions among spiders of different age classes were responsible for the differences in the timing of web construction. This is seen by the absence of significant interactions between spider size class and cage composition in Table 1 (initiation of permanent spiral, $P = 0.23$) and Table 2 (web completion, $P = 0.26$).

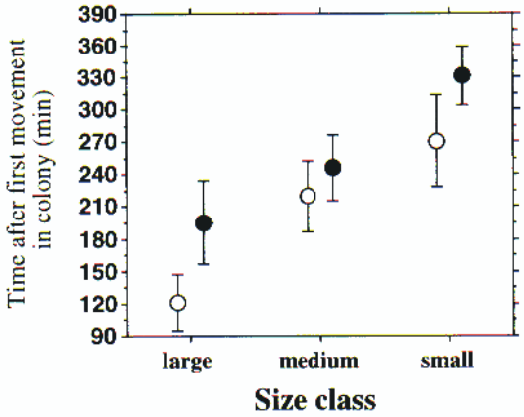

Figure 3.—Means and 95% confidence intervals of the times from when spiders in the colony first began moving to initiation of permanent spirals (○) and completed orbs (●) of the three size classes of spiders (large = 7–10 mm; medium = 4–6 mm; small = 1–3 mm).

DISCUSSION

Smaller spiders began and finished their webs later in the day than did larger spiders. We did not observe orb take-down at the end of the foraging period in this experiment, but in other colonies spiders of all sizes take down their orbs almost simultaneously (Uetz & Jakob pers. obs.), suggesting that the foraging day for smaller spiders is shorter than for larger spiders. The observation that smaller spiders built their webs later in the morning than did larger ones cannot be wholly accounted for by interactions among different size classes of spiders. We found no evidence that large spiders begin the construction of the permanent spiral earlier when medium and small spiders are present in the colony or that smaller spiders delay web construction when in the presence of larger spiders (Table 1).

What may cause the pattern of later orb construction in smaller spiders? Three explanations are possible. First, the effect of past competitive interactions cannot be excluded. We did not use naive spiders, but spiders that had been recently collected from a large colony. Individuals may have learned to avoid interactions with larger spiders and to remain quiescent while larger spiders are active in the colony. Second, even if learning is not involved, aggression between conspecifics may have led to different orb-building strategies for different size classes of spiders over evolutionary time. Third, spiders of different sizes may have different physiological constraints. Temperature, for example, affects spider development, reproduction and other life-history traits (Li & Jackson 1996). A number of species have been shown to prefer particular temperatures (reviewed in Humphreys 1987); for example, *Achaearanea tepidariorum* (C.L.

Koch) placed in a thermal gradient moved to the temperature optimal for web construction (Barghusen et al. 1997). It is possible that warmer temperatures are necessary to trigger orb-building behavior in smaller *M. incrassata spiders*. Spiders of all sizes begin building earlier in the day in warmer weather, and often pause during orb construction when clouds appear (Jakob pers. obs.). A third replicate of this experiment in which direct sunlight hit some cages earlier than others had to be discarded because spiders in the sun built significantly earlier. However, in two lycosid species, juveniles selected lower temperatures than did adults (Sevacherian & Lowrie 1972), which does not support this interpretation of *M. incrassata* behavior. Experiments under controlled temperatures are necessary to test this hypothesis.

These results differ from those in a similar experiment (L. Rayor pers. comm.) in which medium and small spiders together in colonies built an hour earlier than did those in colonies that included large spiders. Her evidence suggests that large spiders interrupt smaller spiders during orb construction. Experimental design may account for the differences in our results. Rayor allowed spiders to acclimate to the experimental colony for several days before data collection. This may have allowed smaller spiders in colonies without large spiders time to learn that they were not likely to be interrupted. In our experiment, colonies were observed two days after establishment, so spiders were not afforded the same opportunity to learn. In addition, Rayor's colonies were larger and not enclosed in cages, and perhaps this had some effect.

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