WHY DO SOME SPIDERS COOPERATE?
AGELENA CONSOCIATA, A CASE STUDY

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SYNOPSIS

I tested the idea that cooperative behavior develops only in tropical spiders because these species exist in an environment that lacks the pressure of competition for prey. The test species was Agelea consociata, an inhabitant of primary rainforest areas in equatorial Africa. It appears that 1) prey availability is potentially limiting in this environment, 2) extinction rates are higher for small colonies than large ones, 3) the majority of the extinctions occur during the rainy seasons, 4) solitary spiders fail to obtain sufficient prey to rebuild their web traps with the frequency necessitated during two three-month rainy seasons, and finally 5) since web trap sizes are not a linear function of the number of individuals within a colony, by living in groups, individuals of A. consociata can reduce their web maintenance "overhead".

Most of the 30,000 species of spiders are highly competitive, territorial and even cannibalistic (Buskirk 1981, Riechert 1982). Only 60 species regularly live in groups. These may be divided into two categories: colonial spiders and cooperative spiders. Reduced aggression and cannibalism are characteristic of both. However, in the case of the colonial spiders social behavior is limited to tolerance of close neighbors. Here individual webs are maintained and defended against intrusion by conspecifics. In addition, there is frequent competition for web placement within the aggregation. In cooperative spiders there is a group web trap, the construction and maintenance of which is shared by all members of a social group. Further, individuals share in foraging activities and those that capture an item of prey are not necessarily the ones that consume it.

Reduced competition for prey among spiders is primarily observed in tropical and semitropical regions although local aggregations of spiders may be observed in those temperate habitats where prey are numerically abundant and temporally constant (Buskirk 1981, Riechert 1981). Figure 1 shows the distribution of colonial and cooperative spiders. Two hypotheses that explain the limited distribution of these more "social" species are: 1. Competition for prey is unnecessary because prey are numerically abundant. Hence, the major obstacle to cooperative behavior in spiders is removed and a certain proportion of the spider fauna are expected to exhibit this strategy (Riechert 1981). 2. Cost/benefit criteria override the need for competition for prey that are present in limited supply. Several studies of colonial species indicate that reduced competition for prey underlies the tolerance exhibited towards adjacent web owners (Buskirk 1975, Uetz and Burgess 1979, Smith 1982, Uetz et al. 1982, Uetz 1985). But similar data have not

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Fig. 1. Distributions of known social spiders. Most localities are field stations.

been collected for the cooperative spider species. In this paper I present my findings on the underlying basis of cooperative behavior exhibited by the spider *Agelena consociata*, an inhabitant of primary rainforest areas in equatorial Africa.

**THE SPIDER**

*Agelena consociata* Denis is a member of the funnel-web-building spider family, Agelenidae. This spider lives in nests ranging from one adult female and her offspring to as many as 1500 females (Figure 2). Each nest is made of a cluster of leaves and branches held together by silk. Attached to the nest are a network of horizontal sheets (the web trap) and a vertical scaffolding which serves to knock prey onto the web trap (Figure 3). The nests are typically associated with shrubs and saplings and are rarely built on the ground. Because electrophoretic analyses completed by Roeloffs and Riechert (unpublished data) show that individuals in adjacent nests belong to the same family groups, I consider a colony to consist of one or more clustered nests. Figure 2 indicates the nest number and size range observed within colonies. See Pain (1964), Darchen (1973) and Riechert et al. (ms) for the ecology, and Krafft (1965, 1966, 1975) for the cooperative behavior of this spider.

**METHODS**

This study was made on the grounds of the Institute for Tropical Ecology near Makokou, Gabon during 4 two month study sessions between Feb. 1982 and June 1984. Three 900 m² plots were established on the M'passe Reserve, and the locations of all nests in the plots were mapped when they first appeared. The following measurements (in cm) were made for each nest: height off the ground, nest volume (height by length by width), web trap area (maximum length by maximum width), scaffolding area (max-
Fig. 2. Example of range of nest sizes and spatial relationships among
such nests in a colony on the M'passe Reserve near Makokou, Gabon. Ver-
tical lines represent nest heights; circles represent nest volumes. Dotted
lines indicate nests that are attached by scaffolding or web-traps.
Fig. 3. Picture showing 2 A. consociata nests in primary rainforest habitat. Vertical lines are scaffolding; the remainder of the silk is the web trap.

imum height by maximum width), and horizontal position within the gridded plot. The fate of each nest was followed during each field session. Each of the 4 seasons exhibited in this area of Africa was thus sampled once: major rainy season, Sept.-Nov.; minor dry season, Dec.-Feb.; minor rainy season, March-May; major dry season, June-Aug. (After Charles-Dominique, 1977 and Hladik, 1978). In addition to weekly censusing for nest presence, all nests below 3m in height were checked for web trap and scaffolding damage.
Insect Behavioral Ecology—87 Riechert

after rains during the minor rainy season of 1982. Rainfall was measured at each nest and was compared with that in a clearing at the Institute. Prey available to small nests (1-4 adult females) was estimated using artificial sticky webs with a surface area equal to that of the average web trap of nests of this size (i.e., 484 cm²). The traps were constructed of hardware cloth, covered with a sticky substance, and captures were sampled each morning during the rainy season.1 Prey availabilities to average sized nests (16 adult females) were estimated through the use of sticky traps measuring 6,525 cm². Each of 5 actual nests outside of the gridded plots were replaced with one of these traps, and sampling was as described above, except that estimates were obtained for each of the 4 seasons.

To establish a regression relationship between nest volume and spider numbers within the nests, 21 nests were collected outside the reserve and were dissected in the laboratory. Individuals were scored as to age class and sex. During each of the 4 seasons, at least 20 nests were also inspected to determine to what extent the age structure of Agelenus varies with season.

Three experiments were completed in the laboratory using spiders collected outside the reserve. In the first, spiders maintained in plastic boxes in groups of 1, 2, 4, and 6 individuals were offered surpluses of prey daily. Record was kept of individual rates of consumption, weight gain, and egg production over a 2 month period. Approximately 50 individuals representing each class were measured. In the second experiment 25 individuals were weighed and placed in .5m³ containers, and after 24 hrs removed and weighed again. The webs each had built during the period were also collected and weighed. In the third experiment, the foraging activity of 5 captive groups of spiders was observed for 18 days. In each group 15 of the 25 individuals were adult females. All spiders were individually marked with fast drying enamel paint. Each colony was observed for thirty minutes each day, following the introduction of prey. Individuals active in web construction, prey capture and feeding were noted.

RESULTS AND DISCUSSION

NULL HYPOTHESIS: NO COMPETITION FOR PREY

Trapping experiments simulating web trap areas associated with one or a few Agelenus indicate that prey are not particularly abundant in this habitat—and note that these data were collected during the season when insects are most numerous (Charles-Dominique, 1977). The paucity of prey available is particularly evident when these data are compared to those from two desert habitats for the New World agelenid, Agelenopsis aperta (Table 1). The same trap area was used in each instance and each estimate was obtained during the time of year when the largest proportion of adult spiders was present.

COST/BENEFIT HYPOTHESIS

From the sticky trap data, it is apparent that the majority of prey available to A. consociata are of smaller size classes—ones that can be readily handled by solitary foragers (Figure 4). So we can rule out one explanation commonly given for cooperative behavior, the joint ability to subdue prey. Comparing the prey intake levels of spiders in groups of dif-
TABLE 1. COMPARISON OF PREY AVAILABILITY LEVELS FOR SHEET WEBS IN
THREE HABITATS. STICKY TRAP = 500 cm² IN AREA. DATA COL-
LECTED FOR PERIOD OF LIFE CYCLE WHEN AGELENIDS ARE MATURING
AND REPRODUCING.

<table>
<thead>
<tr>
<th>Location</th>
<th>Habitat</th>
<th>Mg dry weight/day</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Desert Grassland</td>
<td>27.2</td>
</tr>
<tr>
<td>Arizona</td>
<td>Desert Riparian</td>
<td>73.0</td>
</tr>
<tr>
<td>Gabon</td>
<td>Primary Rainforest</td>
<td>10.8</td>
</tr>
</tbody>
</table>

Different sizes, one further observes that the consumption level per spider
decreases with group size (Figure 5). Two explanations come to mind:
individuals might inhibit the feeding of others, or as group size increases,
individuals expend less energy and hence require less food. Egg production
rates exhibited in this experiment support the first alternative—that conspec-
sics inhibit the feeding activity of nestmates, an effect that increases
with group size (Figure 6). Capture efficiency then does not appear to
underly the cooperative behavior of this species. (Egg production in other
agelelids has been shown vary linearly with prey consumption (Riechert
and Tracy, 1975)).

Based on these findings, solitary individuals would seem to be better off
than individuals living in groups, but inspection of the nest census data
collected over a two year period reveals that solitary individuals are at a
marked disadvantage in the habitat. Smaller nests went extinct significantly
more often than did larger nests.

Fig. 4. Proportion of prey contacting A. consociata webs that can be
readily captured by single penultimate-adult spiders. (Frey lengths equal to
or less than the body lengths of these spiders: Riechert and Luczak, 1982).
Fig. 5. Prey consumption results of feeding experiments for individuals maintained in cages housing respective numbers of individuals. (N = approximately 50 individuals/category). Bars represent mean total weight of prey consumed per day. Standard errors indicated by lines at tops of bars.

The fact that nest numbers are lowest at the ends of rainy seasons (Table 2), suggests a possible reason for cooperative behavior—the frequency of web construction required during the rainy seasons is higher than that during dry seasons and this cost is somehow limiting to solitary individuals. Inspection of the censuses of nests completed following rains
Fig. 6. Mean and standard error of egg production (mg wet weight) per individual with respect to number of individuals in feeding group. Same experiment depicted in Fig. 5.

Relative to precipitation levels indicates that at least 50% of the web trap and scaffolding are destroyed in 84% of the nests when 6mm of precipitation is recorded at the clearing within a 24 hour period. This quantity of precipitation occurring in the clearing is equivalent to 20-40mm in the forest environment—probably due to channeling by branches and foliage. Utilizing 6 years of precipitation records for this same weather station at the Institute, I found that during the 2 major rainy seasons totalling 6 months of the year, *Agelena consociata* must reconstruct their webs 2 out of every 5 days.

**TABLE 2. *Agelena* NEST NUMBERS PRESENT AT END OF EACH SEASON.**

<table>
<thead>
<tr>
<th>Months</th>
<th>Season</th>
<th>Number of Nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept.-Nov.</td>
<td>Maximum Rain</td>
<td>52</td>
</tr>
<tr>
<td>Dec.-Feb.</td>
<td>Low Rain: High Temperature</td>
<td>150</td>
</tr>
<tr>
<td>Mar.-May</td>
<td>Major Tropical Storms</td>
<td>82</td>
</tr>
<tr>
<td>June-Aug.</td>
<td>No Rain: Low Temperature</td>
<td>144</td>
</tr>
</tbody>
</table>
What are the web construction costs relative to the energy levels available to these spiders during the rainy seasons? Given unlimited food in a laboratory context, *A. consociata* expends $360 \pm 1.2J$ per day in the capture of prey and in metabolism ($N=50$ individuals measured over 60 days). An average of $6.5 \pm 1.4 J$ is further put into biomass per day. The construction of a single layer of web trap costs an average of $366.8 \pm 2.8J$. Web construction then doubles the daily energy expenditure of an individual spider. Of the 52 nest sites censused for prey availability, only 27% provided the prey levels necessary to support web construction at the required frequency. And this is probably an overestimate of the number of sites achieving the desired prey level because it assumes that spiders capture all prey that strike the web.

Group living overcomes this limiting energy expenditure because web trap area is not a simple linear function of numbers of individuals (see above and Figure 7). Significantly smaller trap areas per individual are associated with increasingly larger nests. From my observations completed on groups of 25 individuals versus solitary individuals, I found that solitary individuals were active in almost every foraging period (median and confidence intervals = 1), whereas given individuals in groups of 25 were observed foraging every third foraging period (median = 3, 95% confidence interval = 3-4). (By foraging here I mean silk laying and/or prey capture.) In the analysis I did not include feeding on prey already captured.

Thus unlike the findings for colonial spiders, the aggregative tendency

![Fig. 7. Silk investment/individual in the web-trap as a function of the number of adult females present. (Medians and 95% confidence intervals). Probability scores represent results of Mann Whitney test comparisons between adjacent colony sizes.](image-url)
of *A. consociata* is not correlated with high prey densities, but instead the evidence suggests that the frequent web trap damage suffered in the rainforest environment may be the key factor. This appears to severly limit the success of solitary individuals, most of which do not encounter sufficient prey to rebuild their webs with the frequency required. Because web trap area does not appear to be an increasing linear function of the number of foraging individuals in a nest, individual energy investment in the web trap decreases with increasing group size (Figure 7). This of course presumes that larger web traps provide greater prey numbers than predicted for simple linear increases in web area. Data are needed that explore the relationship between trap size and prey encounter rates. In any event, Tietjen (in press) has observed a similar relationship between colony size and web trap area in the New World cooperative spider, *Mallos gregalis*.

There are three adaptations that counter energetic problems caused by frequent rain damage. 1) Spiders could seek web-sites in sheltered locations, 2) they might remain dormant during rainy seasons, and 3) they might live in large groups where individual energetic demands are lower. The first two adaptations are available to temperate spider taxa and commonly occur in temperate areas. Almost all of the temperate spider species are dormant during the winter months and habitat associations of the species studied are significantly non random and often appear to be mediated by environmental concerns (See review by Riechert and Gillespie, 1985).

Cooperative group living, on the other hand, is difficult to achieve in temperate habitats. There must be a continuity of generations, but cold seasons often require long dormant periods and eggs appear to be the most cold-hardy stage in spiders. *Ageletra consociata* does exhibit a continuity of generations through the annual cycle (Table 3). Adults and juveniles are represented in most nests during the course of every season.

In this particular case there are also reasons for the exhibition of cooperative behavior as opposed to dormancy and the refinement of the habitat selection process. Dormancy would have to take place in alternate 3 month periods and during times of highest prey availabilities (Table 4). Further, the dispersal by solitary individuals in the rainforest habitat seems to have a low probability of success (Roelofs, unpublished data). Roelofs observed 5 mortalities suffered as a result of predation events within one hour after the release of a total of 48 spiders. In another experiment, only four new nests (a total of 8 individuals) resulted from the experimental

<table>
<thead>
<tr>
<th>Season</th>
<th>Proportion of individuals</th>
<th>Proport. nests</th>
<th>Both ages present</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Per nest with eggs</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>Juveniles</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean SE</td>
<td>Mean SE</td>
<td></td>
</tr>
<tr>
<td>Major rainy</td>
<td>.12 .03</td>
<td>.88 .03</td>
<td>—</td>
</tr>
<tr>
<td>Minor dry</td>
<td>.58 .005</td>
<td>.49 .005</td>
<td>.17 .98</td>
</tr>
<tr>
<td>Minor rainy</td>
<td>.57 .02</td>
<td>.26 .03</td>
<td>.33</td>
</tr>
<tr>
<td>Major dry</td>
<td>.63 .01</td>
<td>.36 .01</td>
<td>.93</td>
</tr>
</tbody>
</table>

**TABLE 3. AGE CLASS REPRESENTATION IN NESTS DURING VARIOUS SEASONS.**
TABLE 4. ENERGY AVAILABLE TO AVERAGE SIZED COLONIES (16 ADULT FEMALES EXHIBITING A TRAP AREA OF 5600 cm²).

<table>
<thead>
<tr>
<th>Season</th>
<th>Mean joules/day</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>WET:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Major rainy</td>
<td>35097</td>
<td>135</td>
</tr>
<tr>
<td>Minor rainy</td>
<td>17542</td>
<td>415</td>
</tr>
<tr>
<td>DRY:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minor dry</td>
<td>7939</td>
<td>73</td>
</tr>
<tr>
<td>Major dry</td>
<td>2161</td>
<td>34</td>
</tr>
</tbody>
</table>

release of 94 individuals. The exhibition of the third adaptive option by *A. consocista* then does not appear to be fortuitous. Rather, it is favored because of local environmental constraints and the additional fact that these groupings are family units. The data presented here indicate that kin selection probably was not requisite to the development of the cooperative foraging in this spider. It nevertheless may have contributed to the accelerated development of this behavior.

APPENDIX

1A fruit tree banding-compound (Stikem Special: Michel Pelton Co.) provided the sticky coating on the fake web traps. Trap captures were handled as follows. The taxon (Order) and size class (0-4, 4.1-8, 8.1-12 etc. in mm) of all prey were noted. The contents of each sticky trap was placed in a small cloth bag, oven dried at 40° C for 24 hrs, and weighed. The number of days over which the sampling was completed was determined by setting the standard error of mean number of prey at 10% and solving for Ν (number of days).

2Mann Whitney test results: P < 0.0001). The median number of individuals occupying the 37 nests that went extinct was 1 adult spider with a 95% confidence interval of 0-4 adult females. The median group size of the 286 nests that did not go extinct during the course of the study was 16 adult females with a confidence interval of 14-22. These estimates are based on a regression relationship established between nest volume and the number of individuals removed from retrieved nests dissected in the laboratory. The following regression equation has a correlation of 95.8%: Number of Adult Females = .0012 Nest Volume (cm³) –4.13. This is the relationship that showed the highest r value. Hence, it was used rather than total number of individuals in a nest (females + males + juveniles).

ACKNOWLEDGEMENTS

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LITERATURE CITED


