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THE ECOLOGY OF THE COOPERATIVE SPIDER *AGELENA CONSOCIATA* IN EQUATORIAL AFRICA (ARANEAE, AGELENIDAE)[1]

Susan E. Riechert, Rosemarie Roeloffs and Arthur C. Echternacht

Department of Zoology
University of Tennessee
Knoxville, Tennessee 37996, U. S. A.

ABSTRACT

The ecology of the spider *Agelenopsis consociata* in rain forest habitats in Gabon was investigated with reference to factors that might underlie its cooperative foraging behavior. Colonies consisted of local clusters of from one to 27 nests and associated web traps. The composition of individual nests also was highly variable, ranging from one adult spider to as many as 1100 adults. Nest survivorship was a positive function of group size as estimated by the number of adult females in a nest. Analysis of the energy budget of single adult females indicated that the high rate of extinction of small nests might result from insufficient prey availabilities during the two rainy seasons when webs are destroyed on 40% of the days. Individuals associated with larger nests do not experience this energy deficit because individual investment in the web trap decreases with increasing colony size. Dispersal problems may also favor the maintenance of groups: we observed heavy predation on individuals that were released experimentally. On the negative side, individual foraging success and production of eggs decreased with increasing nest size in our experimental groups, perhaps due to the deleterious effects of interference. In addition, we consider that the continuity of generations permitted by the equatorial environment fosters the cooperative life style compared to other adaptations that might be exhibited in response to environmentally imposed energy deficits.

INTRODUCTION

Most work dealing with the evolution of cooperative behavior in spiders involves the mechanisms by which this has been achieved; e.g., changes that occur in spider behavior and patterns of association to permit communal living and the sharing of resources (Shear 1970, Wilson 1971, Brach 1977, Buskirk 1981). Equally important, however, are the ecological influences; external factors that favor the development of cooperative traits. The study of these influences requires field observation and experimentation. That the majority of the communal and actually cooperative spider species are restricted to the lower latitudes, in fact, suggests that some characteristic of the tropical environment is requisite to interindividual tolerance and cooperative behavior in the Araneae which are, for the most part, highly competitive and even cannibalistic.

In an attempt at identifying important parameters we have undertaken an investigation of the behavioral ecology of the highly cooperative spider *Agelena*

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consociata Denis (Agelenidae) which inhabits primary rain forests in equatorial west Africa. Specifically, we consider its local distribution in the rain forest and assess environmental effects on its success in colonies consisting of different numbers of individuals.

AGELENA CONSOCIATA

Agelena consociata, one of two species of *Agelena* that inhabit the Old World tropics, is a funnel web spider that occurs in groups of a few to hundreds of individuals of all age classes (Chauvin and Denis 1965). These individuals share a group nest and a web trap consisting of a flat sheet and attached vertical scaffolding (Fig. 1). Unlike the solitary agelenids, there are multiple retreats, rather than a single retreat, extending into the nest. There is variability both in the composition of the individuals making up the nest and in its physical structure. The latter is formed by the binding of branches and leaves with silk (Pain 1964). Because groups of nests are frequently connected to one another by scaffolding or part of the web sheet, and because individuals move freely among these nests, we define a colony in this paper as consisting of one or more nests in a local area.

Cooperation takes the form of group prey capture, web maintenance and feeding (Krafft 1969). All larger individuals participate in construction of the web trap and scaffolding, though the effort apparently is not a coordinated one (Darchen 1965). Small prey are attacked by single individuals, whereas as many as 25 spiders may be involved in the capture of larger prey that struggle violently in the web (Chauvin and Denis 1965). Only one individual will drag a subdued prey to a retreat. It is during transport that potential competition is observed, with some pushing or shoving evident (our observations and Krafft 1969). Although the winner of the pushing contest has the first opportunity to feed on the prey, it frequently merely deposits the prey in the retreat and moves off without feeding. Twenty to forty spiders may be observed simultaneously feeding on a large prey item (e.g., Krafft 1969 and our observations). We have also observed behaviors that suggest that adults regurgitate digested food to spiderlings.

STUDY AREA

Agelena consociata is probably widely distributed throughout the rain forests of equatorial west Africa, but its range is poorly known. The species has been studied extensively only at a single locality near Makokou, in the Ogooué-Ivindo region of Gabon (Darchen 1975, 1978, 1979, 1980, 1984, Pain 1964, Riechert 1985). Most of these investigations have been conducted at M'Passa, a field station of the Institut de Recherché en Ecologie Tropicale (I.R.E.T.), which is administered by the Centre National de la Recherché Scientifique et Technologique of Gabon. M'Passa is located at approximately 00°34′ N latitude, 12°50′ E longitude, on the west bank of the Ivindo River about 10 km southwest of Makokou. The station, which lies at an average elevation of about 500 m, is part of a 13,000 hectare United Nations Biosphere Reserve and is, thereby, afforded at least nominal protection from human disturbance.

Fig. 1.—*Agelena consociata* colony showing two nests (N) and associated web trap (W), scaffolding (S), and nest retreats (R). Many more retreats are present than indicated.

With the exception of a laboratory clearing, the entire reserve is covered by closed primary or old secondary evergreen rain forest. Our investigations were conducted in a 140 hectare area of the reserve which has been divided into a grid of one hectare quadrats, each 100 m on a side and bounded by paths about 1 m wide. The terrain is generally flat, but slopes gently from the northwest to the Ivindo and Nyame Pendé rivers to the southwest. Darchen (1980) identified four types of forest within the grid system at M'Passa. Two of these can be designated as layered forest and two as unlayered. The layered forests are distinguished by differing heights of the understory, and the unlayered forests by differences in the density of shrubs and vines under the tree canopy. A profile of the annual climatic cycle at M'Passa is presented in Figure 2, together with seasonal trends in insect biomass derived from those reported by Charles-Dominque (1977) and our own data. Precipitation at M'Passa is very unevenly distributed over the year and is the basis for recognizing four seasons (Charles-Dominque 1977, Cruiziat 1966, Hladik 1978). The area receives an average of 1691 mm of precipitation annually, nearly 40 per cent falling during the period September-November. This is the major wet season. It is followed by a minor dry season, December-February, which is characterized by less precipitation and maximum insolation. The minor wet season of March-May is a time of "important rainfall and tropical storms" (Hladik 1978). Finally, the months of June-August constitute the major dry season with minimum precipitation (less

Fig. 1.—*Agelena consociata* colony showing two nests (N) and associated web trap (W), scaffolding (S), and nest retreats (R). Many more retreats are present than indicated.

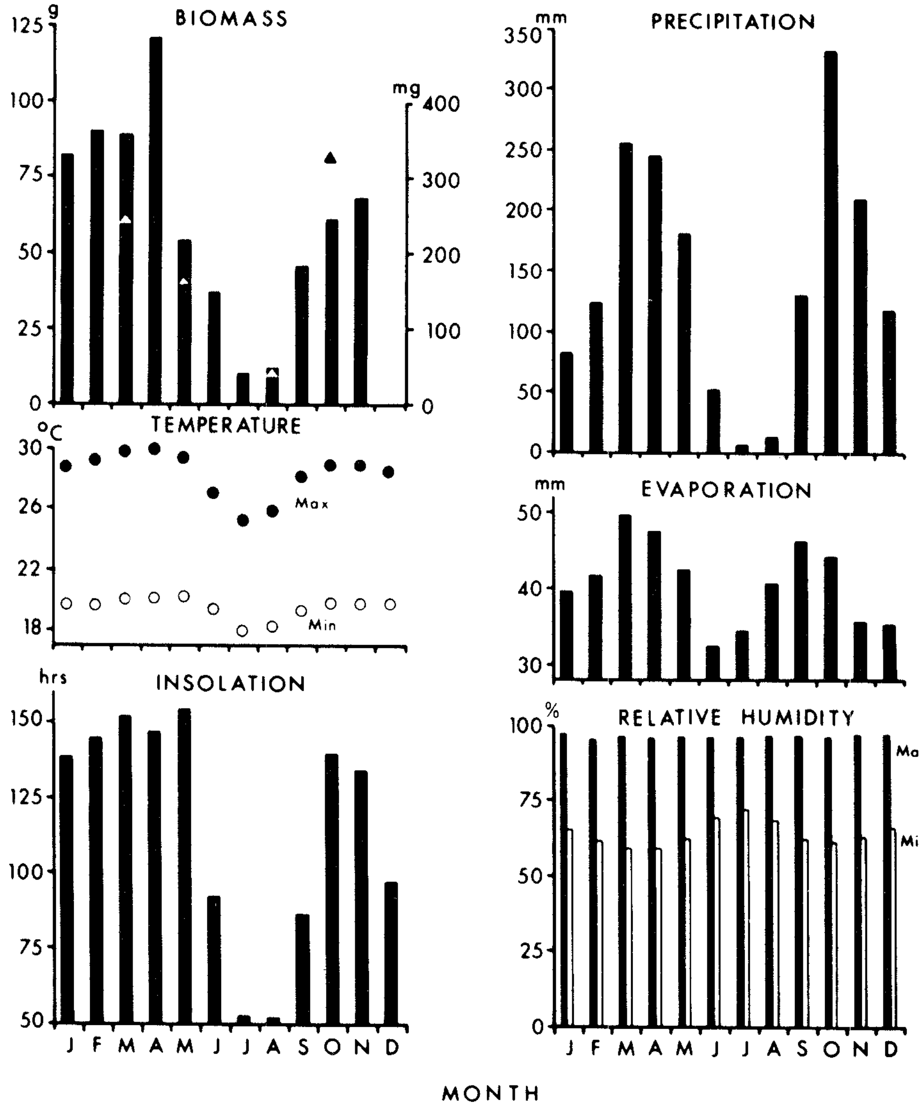

Fig. 2.—Seasonal variation in insect biomass and mean monthly climatic variables at M'Passa. Climatic data are from records of the Gabonese Meterological Service station at Makokou. Insect biomass is expressed as (bars) monthly means (except December) of grams dry weight of daily light trap collections (from Charles-Dominque, 1977, Fig. 10), and as (triangles) milligrams dry weight per trap per day (this study; see text for details).

than 5 percent of the annual mean), but also minimum temperatures and insolation. Because of the constantly overcast skies, relative humidity remains high and evaporation low during this season. As might be expected at a locality so near the equator, monthly variation in temperature is slight, mean monthly temperatures ranging from 21.7°C in June to 25°C in April. *Agelena consociata* is active throughout the year at this locality.

METHODS

Colony Structure and Habitat Association.—Three 9 hectare study areas were established within the reserve (Fig. 3). Two of the locations were selected to provide data on spider habitat associations in layered and unlayered forest types. The third area is representative of the habitat used by Darchen in his 1980 study of the distribution of *Agelena consociata* in the reserve. Each study area was inspected for colony locations by walking all 100 m transect lines within the areas and traversing each one hectare quadrat within each area at 30 m intervals. The locations of all nests in the plots were first mapped in February 1982. The following measurements (in cm) were taken on each nest: height off the ground, nest volume (maximum height by length by width), web sheet area (maximum length by width), vertical scaffolding height and distances to other nests within the colony. Twenty-one nests were collected off of the reserve for use in regressing nest volume against spider numbers. The age and sex of each individual were tallied as they were removed from the nests. We used the resulting regression coefficients in estimating individual numbers in nests censused on the study areas where destructive sampling was not possible.

In addition to the web structure measurements, the following habitat features were recorded at 10 cm intervals along a 2 m transect beneath each web: the presence of leaf litter under the nest, the presence of tree cover, the presence of vegetation within 1 m above the nest, the presence of non-herb vegetation below the nest, the presence of narrow (< 10 cm), medium (10-20 cm) and broad leaves (> 20 cm) below and above the nest, numbers of leaf layers below the nests, numbers of branches [narrow (< 1 cm), medium (1-4 cm), wide (4.1-16 cm) and giant (> 16 cm)], below the nest and the presence of herbs. The transect was oriented such that its 50 cm mark was positioned at the center of the nest and it paralleled the longest axis of the web trap. The distance from the nest to the canopy was estimated using a rangefinder.

For each nest within the two main study areas, a random site within the reserve was located by picking random coordinates. The line intercepts were repeated at each of these sites using the compass orientation determined for the line intercept of the actual site and the respective web heights in the positioning of the sample. These sites and their corresponding nest sites were *not* treated as paired samples in subsequent analyses. Multiple discriminant analyses were applied to the transect data to determine to what extent the habitat characteristics of nest sites were representative of the general habitat and how habitat utilization might vary with forest type.

Environmental Correlates.—Three additional environmental correlates were considered: solar radiation, precipitation, and prey availability. At all nest sites and their corresponding random sites within the two main study grids, solar radiation striking the web at hourly intervals was scored at 0, partial, or total, through visual censusing. In addition, precipitation readings were taken at all nests and associated random locations that were < 3 m in height. Rain gauges were placed directly above or adjacent to the nests and at comparable nest heights in the random sites. These precipitation estimates were referenced to those provided by a rain gauge placed in the laboratory clearing. This allowed us to use the station's precipitation records in estimating the number of days per rainy season in which web-damaging rains occur.

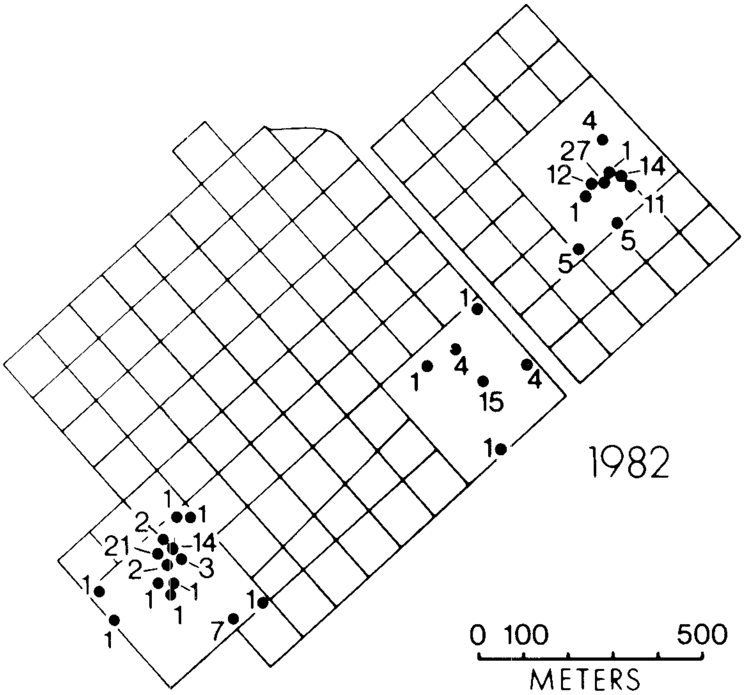

Fig. 3.—Distribution of colonies of *Agelena consociata* in study plots at M'Passa at the initiation of censusing in February 1982. Numbers refer to numbers of nests in the respective colonies. Plot 1 is in the center, 2 in the upper right, and 3 in the lower left of the figure.

Five nest sites, each from a different colony, were selected outside the study areas for prey availability determinations. The nests were removed and sticky traps measuring 6,525 cm^2 were substituted. The trap consisted of horizontal and vertical sheets of hardware cloth approximating the linear dimensions of the web sheet and scaffolding, respectively, of the average *A. consociata* web trap. The entire surface was coated with a thin coat of a sticky tree banding compound (Stikem Special: Michel Pelton Co.). Random trap locations corresponding to each actual nest-site were chosen as in the vegetation analyses. Potential prey were collected from the traps each morning during the course of the censusing, which was carried out in each of the four seasons. All prey caught on the traps were scored as to Order and size class (0-4, 4.1-8, 8.1-12, etc. in mm). The contents of each trap were placed in a small cloth bag and oven dried at 40°C for 24 hours (The sticky material evaporated during the course of the drying process). The samples were then weighed. The number of days over which the sampling was completed for each season was determined by setting the standard error of mean number of prey at ten percent and solving for number of days (13-14 days in different seasons).

Extinctions.—During the course of each of 4 two month field seasons the fate of each nest in the grids was followed through weekly censuses. The sampling periods were: February-March (Minor Dry Season), 1982; June-July (Major Dry Season), 1982; October-November (Major Rainy Season), 1983; and April-May (Minor Rainy Season), 1984. As new nests were found during the course of censusing, web and habitat measurement were collected as described for the initial sample. At the beginnings and ends of each 2 month census period, nest volume and web area measurements were repeated. In addition to the weekly censuses, nests below 3 m in height were checked for web sheet and scaffolding damage following rains during the Minor Wet Season of 1982.

Energy Budget.—A combination of field and lab studies were used to complete comparative energy budgets for individuals at small (1-4 adult females) versus large (>25 adult females) nests. We used sticky trap collections of potential prey in estimating energy availability. The data collected to show seasonal variability in prey availability were used in the case of the large nests. Using the same methodology, sticky traps providing a surface area of 484 cm^2 (the average trap area associated with small nests) were also censused for prey numbers and composition.

Estimates of prey consumption rates under unlimited food, the frequency of foraging activity, and energy expenditure in construction of the web trap were obtained from laboratory studies. Individuals maintained in plastic boxes in groups of one, two, four and six individuals, respectively, were offered an abundance of prey (moths, flies and disabled crickets) on a daily basis. Record was kept of individual rates of consumption, weight gain, and egg production over a two month period. Approximately 50 individuals representing each class were measured. In the second experiment, 25 individuals were weighed and placed in $0.5m^3$ containers. After 24 hrs, the individuals were removed and reweighed. The webs each had built during the period were also collected and weighed. The third experiment consisted of eighteen days of observation of the foraging activity of five captive groups of individuals. Each group consisted of 25 individuals, 15 of which were adult females. All spiders were individually paint-marked using a fast-drying enamel paint. Thirty minute watches were made of each group following the introduction of prey once a day, and individuals active in web construction, prey capture and feeding were noted.

Microbomb calorimetry was used in making mass conversions of joules and in estimating what proportions of available prey were available for consumption by the spiders. Twenty-five individuals of each of the major prey orders contacting *Agelena* webs were collected, weighted, killed by freezing, dried as for the sticky trap samples, and reweighed. Prey wet weight averaged 2.32 times dry weight. The joule equivalent of 1 mg dry weight was 20.83 averaged over all prey types. Finally, an average of 5.56% of the prey was ash. This quantity was subtracted from the sticky trap estimates in calculating prey availabilities.

Population Structure.—During each of the four field study sessions, at least 20 nests were inspected to determine to what extent the age structure of *Agelena* varies with season. Individuals were removed as the nests were dissected and were tallied as to approximate age (spiderlings, juveniles, penultimates and adults) and sex.

There is no known record of active dispersal by *Agelena consociata,* nor did we observe such a phenomenon during the course of our study. We did observe the destruction of nests by rain, falling objects and animal movements (birds and mammals). A release experiment was thus performed to assess the survivorship of individuals that lose contact with their nests during such stochastic events. In the experiment, all preexisting *Agelena* nests within a 50 m radius of a chosen site were recorded and marked with plastic flagging. Spiders were collected from five different nests from other areas of the forest, were paint marked and then released using the following protocol: 1) Forty-eight spiders were released individually and their movements followed until each had moved out of the cleared release area; 2) The remaining spiders were released in groups of up to five individuals. In the latter case individual movement within the release area was not followed. Rather, a daily search was made for new nests built by released spiders within the area. The location, size, and distance from the release site were recorded for each new nest along with the identity of the resident spider.

Genetic relatedness of spiders within nests and colonies was assessed using electrophoretic techniques. Twenty-five spiders were collected from each of one to three nests/colony for 30 colonies to allow estimation of degree of relatedness for individuals within the same nest, the same colony, and separate colonies. The collected spiders were subjected to starch gel electrophoresis in the Population Genetics Laboratory at the University of Tennessee. Whole individual spiders were ground using the methodology described in Selander et al. (1971). The gel electrophoresis techniques used were similar to those described in the same paper. The following loci were assayed: Esterases 1 and 2 (EST1 and EST2), Fumarase 1 and 2 (FUM1 and FUM2), Galactosaminidase (GAM), Glutamic Oxaloacetic Transaminase 1 and 2 (GOT1 and GOT2), α-Glycerophosphate Dehydrogenase 1 and 2 (GPD1 and GPD2), β-N-Acetylglucose-aminidase (HEX), Isocitrate Dehydrogenase (IDH), Lactate Dehydrogenase 1 and 2 (LDH1 and LDH2), Malate Dehydrogenase (MDH), Malic Enzyme (ME), Mannose Phosphate Isomerase (MPI), Octanol Dehydrogenase (ODH), Peptidase (PEP), Phosphoglucose Isomerase (PGI), and Superoxide Dismutase (SOD). Of these, three were polymorphic: PEP (three alleles), EST1 (three alleles), and EST2 (two alleles).

RESULTS

Colony Structure.—Statistics pertaining to colony structure are presented in Table 1 for the 29 colonies in existence at the time of the initial census (Fig. 3). Colonies frequently were represented by more than one nest, and in 40 per cent of these multiple cases nests were interconnected by either a shared web sheet or scaffolding. Because it was impossible to determine the number of individuals occupying different nests without destruction of the nest, a relationship was established between the numbers of individuals and nest volume, using nests collected off the reserve. We found that the highest correlation between nest volume and colony size was achieved when only adult female occupants were included ($r^2 = 96.8\%$). All of the colony size estimates used in this paper thus were calculated from the following regression relationship:

$$\text{No. of Adult Females} = 0.0012\ \text{Nest Volume}\ (\text{cm}^3) - 4.13$$

Habitat Association.—The results of the discriminant analyses comparing the vegetation characteristics of actual nest sites with random sites are presented in Figure 4. Colony habitat associations are apparently non-random, differing markedly in character from the general habitat available. Inspection of the discriminant function coefficients representing each habitat variable indicate that the nests tend to be constructed above multilayered shrubs under a full tree canopy, but without branches immediately overhead (i.e., within 1 m).

Table 1.—Basic colony statistics for 29 colonies of *Agelena consociata*

COLONY STRUCTURE

	Mean	Standard Error	Range
Number Nests/Colony	5.3	1.6	1-27
Nest Volume (cm^3)	53094.2	879.4	120-1,848,000
Web Area (cm^2)	5726.9	129.1	192-63,000
Scaffolding Height (cm)	131.4	0.7	0-550
Adult Females/Nest*	16	14-22	0-2213

**Median and 95% confidence interval based on regression relationship: No.* = 0.0012 (Nest Volume)-4.13. (r = 0.958)

NEST HEIGHT

Study Area	Forest Type	Nest Height Mean	Nest Height Standard Error
Plot 1	Layered, Low Understory	163.9	4.3
Plot 2	Unlayered, Lianas	287.6	1.7
Plot 3	Layered, High Understory	410.8	6.4

Nest height varies with colony location in the forest (Table 1b). Nests are highest in Plot 3 (Fig. 3) characterized by understory with little shrubbery. Nests are lower in forest in which the understory is in the recovery phase (Plot 1) and intermediate in the closed forest characterized by lianas and fallen trees (Plot 2). Despite the differences in nest height, spider use of habitat appears to be similar in the three habitats. Of particular interest is the comparison between spider utilization of habitat features in our first two study plots with the section of forest lacking an understory (Plot 3) which was characterized by Darchen (1980) as prime *Agelena* habitat. The nests measured in this third grid were not included in the initial discriminant analyses. Rather, scores for each nests were calculated post facto using the discriminant coefficients derived from the analysis for each habitat feature measured. Discriminant scores for nests censused in Plots 1 and 2 did not differ from those for the higher nests (Mann Whitney test, $P > 0.25$).

The vegetation features utilized by *Agelena consociata* might be predicted on the basis of web structure alone, because the nest is constructed of curled branches and leaves and must be supported by some underlying structure. In addition, the vertical scaffolding requires an empty space but with points of attachment present. There are, however, possible additional influences on habitat association. Incident precipitation at actual nest sites, for instance, is significantly less than that encountered at the corresponding random sites in the reserve ($N = 46$, Sign Test: $P < 0.001$; median ratio of precipitation at nest sites to random sites = 0.61). The variance in rainfall at random sites does not differ significantly from that characteristic of nest sites (Siegel Tukey Test: $P < 0.35$). In one season, at least, prey numbers and biomass are significantly higher at nest sites than at random sites (Table 2). Solar radiation reaching the nests was estimated by visiting each nest and associated random site once during each of 9 daytime hour intervals (clear days only). The differences between light counts at nest sites and associated random sites was highly significant (Sign Test: $P < 0.0001$), with more direct solar radiation hitting actual nests (Mean = 3.12 ± 0.02 intervals) than random sites (Mean = 1.94 ± 0.02).

Extinctions.—The marked variability in colony sizes and nests sizes in particular suggests a corresponding variability in colony success in the rain forest

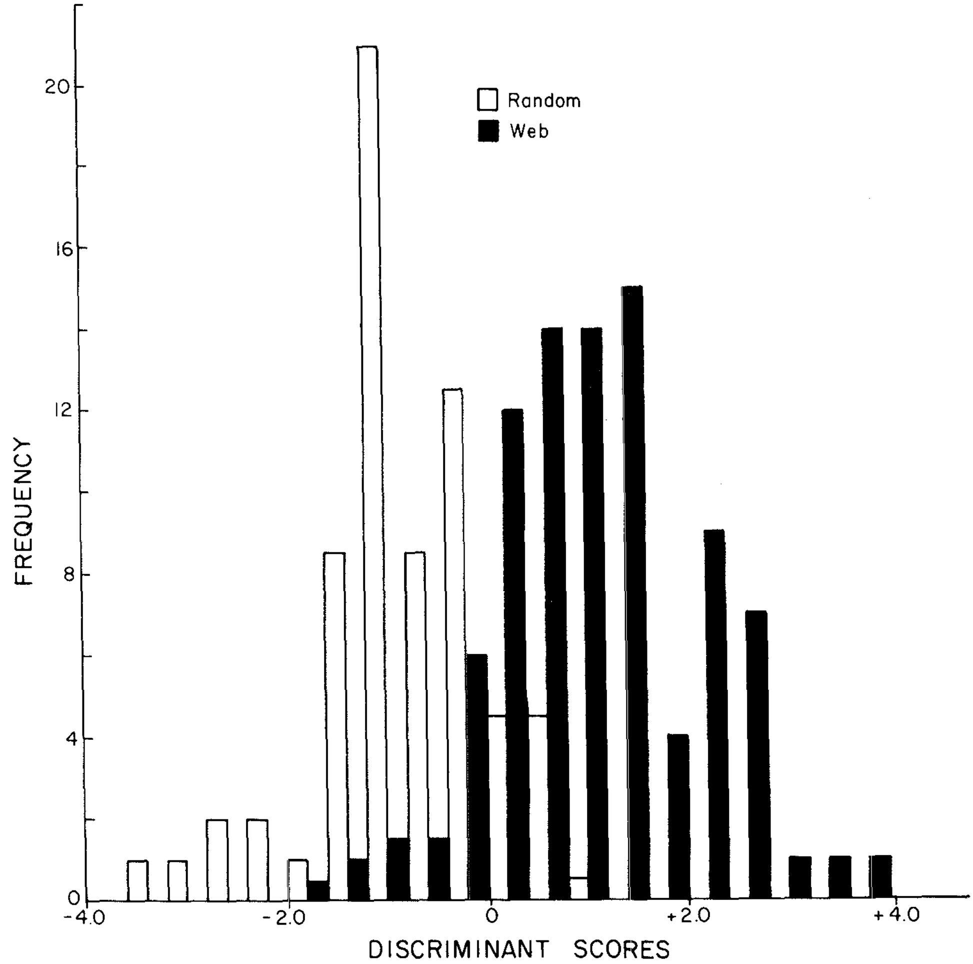

Fig. 4.—Results of discriminant analyses of habitat variables at *Agelena consociata* nest sites and random sites in the original study plots (two upper right plots, Fig. 3). Scores represent sample placement on the basis of vegetation characteristics at a particular site.

habitat. Inspection of the nest census data collected over the two year period of this study shows that smaller nests went extinct significantly more often than did larger nests (Mann Whitney Test: $P < 0.0001$). The median number of adult females occupying the 37 nests that went extinct was 1 with a 95 per cent confidence interval of 0-4 adult females/nest. The median number of adult females occupying nests that were not lost during the censusing was 16 with a 95 per cent confidence interval of 14-22. Most of these extinctions occurred during the two wet seasons, as is indicated by the nest numbers present at the end of the respective seasons (Table 3). This is despite the fact that larger nests tended to receive more precipitation than did smaller nests ($r = 0.38$; $P < 0.05$). Our nest and web censuses following rains in which precipitation levels were recorded both at the sites and in a nearby clearing shows that at least 50 per cent of the web trap and scaffolding are destroyed at 84 per cent of the nest sites when 6 mm of precipitation is recorded at the clearing within a 24 hr period. This quantity of rain is equivalent to between 20 and 40 mm of rainfall at the

Table 2.—Comparison of prey encounter estimates for paired *Agelena consociata* nest sites and random sites over 4 seasons. Mean and standard errors mg dry weight/dry. Probabilities refer to results of sign tests. NS = Non-significant.

Season	Nest Sites	Random Sites	Probability
	PREY BIOMASS		
Major Wet	321.1 4.8	318.9 4.1	NS
Minor Wet	240.9 6.7	234.4 3.4	NS
Minor Dry	176.4 1.6	129.2 1.2	P<0.0001
Major Dry	48.0 0.7	30.6 0.5	NS
	PREY NUMBERS		
Major Wet	65.6 0.6	62.7 0.4	NS
Minor Wet	58.4 0.4	71.1 0.4	NS
Minor Dry	49.5 0.2	36.8 0.2	P<0.0001
Major Dry	38.1 0.2	39.6 0.2	NS

actual nest sites due to channeling by branches and foliage. Utilizing six years of precipitation records for the clearing site on the reserve, we found that during the two wet seasons totaling six months of the year, such web trap destruction occurs on the average every two out of five days.

Energy Budget.—Solitary *Agelena consociata* expend an average of 360 ± 1.2 J per day in the capture of prey and in metabolic expenditures (N = 50 individuals measured over 60 days). An average of 6.5 ± 0.4 J is further put into biomass and egg production per day when food is presented *ad libitum.* The construction of a single layer of web trap costs an average of 366.8 ± 2.8 J. Web construction, then, doubles the daily energy expenditure of an individual spider.

Of the 52 nest sites censused for prey availability, only 27 per cent provided the prey levels necessary to support web construction by a solitary individual at the required frequency of two times/five days. This is, in fact, an overestimate because it assumes that a spider captures all prey that encounter its web.

By living in groups, *Agelena consociata* can overcome this limiting factor, because web trap area in this social group decreases with increasing numbers of individuals (Table 4). Thus, significantly smaller trap areas per individual are associated with increasingly larger nests. Our activity census data indicate that solitary individuals in captive nests were active in silk laying or prey capture in every foraging period (median and 95 per cent confidence interval = 1), whereas individuals belonging to nests containing 25 spiders were active only every third foraging period (confidence interval = 3-4).

Population Structure.—The survivorship of *Agelena consociata* nests and colonies may also be affected by population structure. Nest censuses show that within the same season the proportion of adult males represented relative to females varies considerably from nest to nest (range = 0-58 per cent of the adult

Table 3.—Number of *Agelena consociata* nests present in study grids at end of each season.

MONTHS	SEASON	NUMBER OF NESTS
Sept-Nov	Major Wet	52
Dec-Feb	Minor Dry	150
Mar-May	Minor Wet	82
June-Aug	Major Dry	144

Table 4.—Change in web investment per adult *Agelena consociata* (cm^2) with number of individuals in a colony. Significant changes (Mann Whitney test) denoted by broken lines. ($1 = p < 0.05$; $2 = p < 0.001$).

NUMBER OF INDIVIDUALS	MEAN	STANDARD ERROR	NUMBER OF NESTS	
1- 5	930	421	43	
6- 25	738	158	47	1
26-125	400	139	27	
126-625	333	151	17	2
626-3125	14	20	3	

spiders present). Further, significantly more small nests (0-4 adult females) had no males than larger nests (> 4 adult females: Chi square test, $X^2 = 4.64$, $DF = 1$, $P < 0.05$). With such low numbers of males, smaller nests and single nest colonies may become extinct because there is no sperm supply and hence no production of offspring.

It is improbable that males immigrate from neighboring nests to supplement a declining population. This conclusion is based both on the results of our release experiments and genetic studies. After 4 weeks of following the release of 94 individuals onto the rain forest floor, a total of only 8 spiders had relocated and all of these relocations constituted newly formed nests. Ten per cent of the 48 individuals whose dispersal was tracked after release, in fact, suffered predation within the first hour after release. Electrophoretic analyses completed on these populations also indicate that there is no migration between colonies. Nei's (1972) Genetic Identity scores (I) were calculated for attached nests ($I = 0.9982 \pm 0.001$) and unattached nests (0.9982 ± 0.001) within colonies. Therefore, individuals in nests within a colony are almost identical genetically and colonies may consist of single families. Similarly high genetic identities among family groups have been reported for other taxa (e.g., marmots, Schwartz and Armitage 1981). However, nests separated by as little as 38 m (and occurring in different colonies) have lower Genetic Identity scores ($I = 0.9340 \pm 0.005$) and may be fixed for different alleles at the same polymorphic locus.

Predation Efficiency.—One of the major explanations given for cooperative behavior is the increased efficiency of feeding, particularly on large prey [See Buskirk (1981) for review]. From the sticky trap data, however, 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 (Fig. 5). Furthermore, we found that food intake per spider decreases with group size (Fig. 6). This could reflect an inhibitory effect of conspecifics on the feeding level of associated individuals or it may indicate that as group size increases, individuals expend less energy and thus require less food. In the same experiment, egg production rates decreased with increasing group size (Fig. 7). This supports the first alternative: that conspecifics inhibit the feeding activity of nest mates, an effect that increases with group size (Fig. 7). Capture efficiency, then, does not appear to underly the differential extinction of smaller nests.

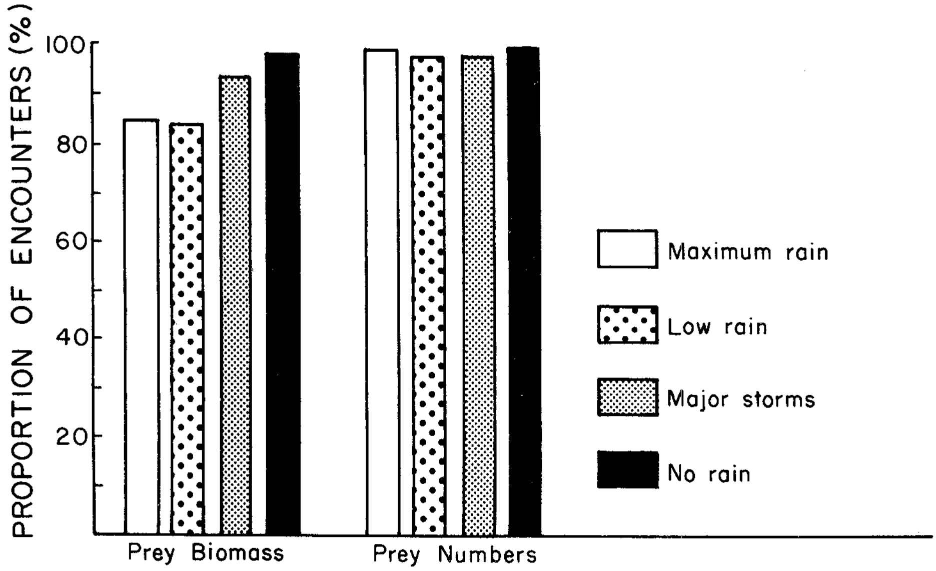

Fig. 5.—Proportion of prey contacting *Agelena consociata* webs that can be readily captured by single penultimate-adult spiders (prey lengths equal to or less than the body lengths of these spiders: Riechert and Luczak 1982).

DISCUSSION

The behavior of an individual is governed by the degree of relative advantage that behavior affords. This advantage is generally expressed in terms of individual fitness or the number of surviving offspring an individual produces. Cooperation in foraging, nesting, and defense against predators, however, does occur and the origin of such behavior is difficult to explain by natural selection operating on the individual. From a game theoretic view, if a population initially consists of competitors, for instance, it is difficult for an altruistic mutant gene to invade, because the payoff to the competitor when interacting with a cooperative individual would always be higher (e.g., Axelrod 1984).

Three conditions have been identified as contributing to the evolution of sociality: mutual benefit to the interacting individuals, kin selection, and reciprocity. Under the first condition, cost/benefit factors are such that it pays individuals to interact in a cooperative manner. This would be the case if the majority of prey available to *A. consociata* were larger in size than could be readily captured by solitary individuals. [See Michener (1974) and West-Eberhard (1975) for examples.] Under kin selection, relatives share more genes than the population at large and thus, by aiding kin, individuals increase the survival of copies of their own genes (Hamiton 1964a,b, Dawkins 1976). Reciprocity denotes the exchange of altruistic acts occurring with a time lag: individual A benefits B on day one and B benefits A at some later date (Trivers 1971). If there are repeated interactions between individuals, and individual recognition in larger groups, reciprocity can invade a competitive system, but only if the invasion is by groups of individuals (Axelrod 1984).

Spiders are a particularly interesting group within which to examine the underlying causes of cooperative behavior because the vast majority of the species are highly competitive and even cannibalistic towards conspecifics. Why is the

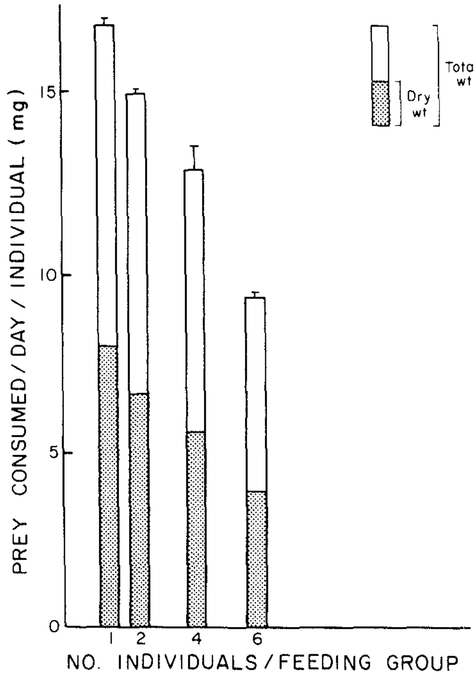

Fig. 6.—Results of Prey consumption feeding experiments for individual *Agelena consociata* maintained in cages housing indicated number of individuals (N = ca. 50 individuals per category). Bars represent mean total weight of prey consumed per day; standard errors indicated by lines at tops of bars.

exhibition of cooperative behavior limited in this group to the tropics and which if any of the three conditions underlies it? Some clues to these problems are provided in this ecological study of *Agelena consociata.*

A major limiting factor to the success of individual funnel spiders in the rain forest habitat of Gabon is heavy rainfall. The energetic deficit incurred through frequent web trap replacement during these periods is not balanced by food intake at the majority of nest sites. Three adaptations might have been exhibited by *Agelena consociata* in response to this energetic constraint. 1) Spiders might remain dormant during the rainy seasons. 2) Habitat selection might be refined such that greater protection from rain damage is afforded. 3) Spiders might live in family groups where individual energy expenditure in maintenance of the web trap and other foraging activities is markedly reduced. The first two adaptations are typically exhibited by temperate spider species, but, at least the first is not particularly well suited to *A. consociata.* Spiders would have to be dormant during six months of the year alternating three months of activity with three months of dormancy. Besides the logistical problem associated with cuing activity on and off on such a schedule when day lengths and temperatures vary little, there is the additional fact that this dormancy would coincide with times of maximum insect densities (Table 2). Spiders would, by necessity, be dormant during periods when they could best maximize their intake of prey. (Note that *Agelena consociata* is the only common sheetline weaver in this rain forest study site.)

Agelena consociata exhibits a non-random association with habitat features, one which does lend some protection from precipitation. The major obstacle to increased use of habitat selection criteria to this species, however, is the apparently high cost of dispersal. The release experiments demonstrate that *A. consociata* moving across the forest floor suffer a high mortality rate to ants and

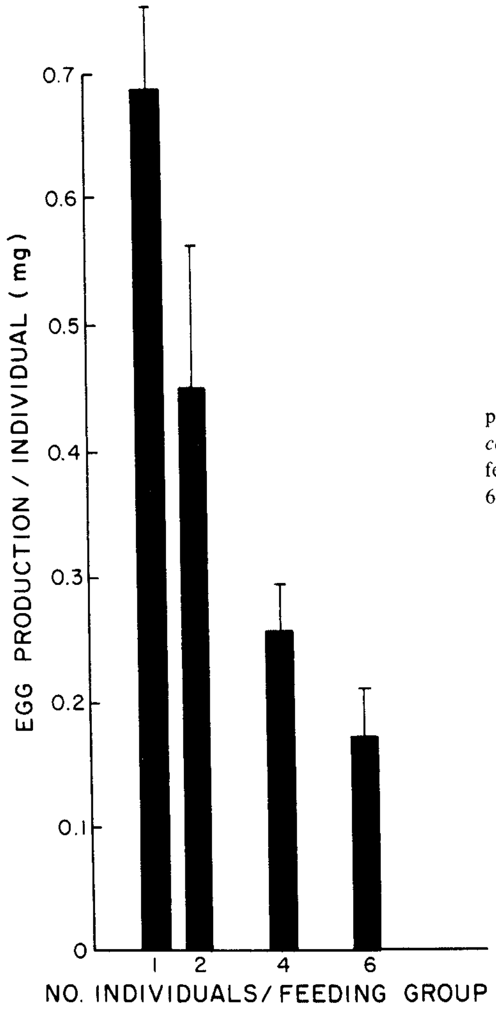

Fig. 7.—Mean and standard error of egg production (mg wet weight) per individual *Agelena consociata* with respect to number of individuals in feeding group (same experiment as depicted in Fig. 6).

other invertebrate predators. All indications are that if dispersal does occur, it is a rare event. We consider that the break up of colonies into smaller nests is mainly achieved through the action of rain and falling limbs. Colonization, on the other hand, probably involves passive transport of pieces of nests by bats that live in them and by birds and mammals that may occasionally fly or walk through them.

The long term cohesiveness of family groups is favored by the rain forest environment for several reasons. First, the cost of dispersal is high. Second, the apparent energetic advantage of construction of a group web trap overcomes the limiting constraint of rain damage to nest success. These benefits apparently outweigh the negative effects of group living on individual foraging efficiency observed in our laboratory experiments. Finally, and what we consider key to the tropical dilemma, is the fact that in this equatorial environment, year around moderate temperatures allow a continuity of generations (Table 5) that is difficult to achieve by the spiders in temperate environments. By Occam's razor, continuous colony function permits the evolution of cooperative behavior with the minimum of adaptive modifications (*sensu* Wilson, 1975). It is this continuity

Table 5.—Age class representation of *Agelena consociata* in nests by seasons.

SEASON	PROPORTION OF INDIVIDUALS PER NEST				PROPORT. NESTS WITH EGGS	PROPORT. NESTS BOTH AGES PRESENT
	ADULTS		JUVENILES			
	MEAN	SE	MEAN	SE		
Major Rain	0.12	0.03	0.88	0.03	—	1.0
Minor Dry	0.53	0.01	0.49	0.01	0.17	0.98
Minor Rain	0.57	0.02	0.26	0.03	0.33	1.0
Major Dry	0.63	0.01	0.36	0.01	0.93	1.0

that explains the fact that cooperative behavior is limited in spiders to tropical areas.

Both mutual benefit and kin selection may underly the cooperative behavior exhibited by *Agelena consociata*. An influence by reciprocity is less certain since work by Krafft (1971, 1974) shows that there is no individual recognition, and group sizes are frequently too large for the action of this phenomenon in the absence of individual recognition. Delineation of the relative contributions of mutualism and kin selection awaits further work, particularly with colonies of intermediate-large size. Kin selection may not have been requisite to the development of cooperative behavior in this species because of the marked benefits associated with group living in the rain forest environment, but inclusive fitness effects might have accelerated the development of the system.

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