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EFFECTS OF COLONY SIZE ON WEB STRUCTURE AND BEHAVIOR OF THE SOCIAL SPIDER *MALLOS GREGALIS* (ARANEAE, DICTYNIDAE)[1]

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ABSTRACT

Groups of size 1, 2, 5, 10 and 20 *Mallos gregalis* were monitored under laboratory conditions with the aid of a computer-controlled digital camera. Data collected included a measure of the density and complexity of the silk comprising the nest, as well as activity levels and occupation of space within experimental arenas.

Average web density and complexity was related to colony size, with the larger colonies building more complex nests. I suggest that the greater web complexity would allow larger colonies greater opportunities for the exploitation of marginal habitats. The webs built by the two smaller groupings were similar to those built by solitary dictynids and indicated that *M. gregalis* may be a facultatively-social spider. An estimate of mean silk deposition per spider indicated that members of the larger colonies exerted less effort in web construction than spiders in the two smaller groupings.

Colony activity was related to group size and exhibited evidence for a group effect in the patterning of activity bouts. It is possible that this would aid in coordinating colony behavior. Measures of both web structure and colony activity indicated that the changes in colony behavior were not due to a simple arithmetic effect (e.g., size 20 colonies were neither twice as active nor were their webs twice as complex as colonies of size 10).

INTRODUCTION

Although most spiders are solitary, aggregating only early in life or during mating, a few species are social (Shear 1970, Kullman 1972, Burgess 1978, 1979a, Buskirk 1981). Unlike the groups seen among the insect societies, no araneid associations studied to date show evidence of ethological nor morphological caste systems (Wilson 1971, Burgess 1979b). For this reason, studies of social spiders must confront the problem of how such complex groupings are behaviorally organized. The present laboratory study describes some organizing features of colony behavior in a social spider, *Mallos gregalis,* especially the effects of colony size on the patterning of activity, nest complexity and web construction.

Mallos gregalis is a social species living in colonies that may cover three-quarters of an 18-m tree with webbing. Up to 20,000 individuals of both sexes and various stadia may inhabit such nests (Diguet 1909a, 1909b, Burgess 1979b, Uetz 1983). Predation, feeding and web construction are communal, with little or no cannibalism occurring among conspecifics (Witt et al., 1978).

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The web is an intricate, sheet-like affair, superficially resembling that of tent caterpillar larvae (*Malacosoma* spp). The outer surface, (the primary prey-capture site), has silk-reinforced tunnel openings to the web interior, silk-reinforced runways, water-resistant papery areas, loosely-woven cribellate silk sheets, as well as the remains of their prey, primarily muscid flies. The web interior has numerous silk-lined tunnels and chambers which gives it a spongy appearance. Spiders spend most of the day within these chambers, moving to the surface only when it is disturbed by struggling prey. Within the web *M. gregalis* courts, mates, constructs egg sacs and deposits silk to reinforce tunnels and chambers. At the surface of the nest spiders capture prey, feed communally, eliminate excreta and deposit silk for web expansion (Tietjen 1986).

MATERIALS AND METHODS

General Methods.—Approximately 350 *Mallos gregalis* from a colony collected near Guanajuato, Guanajuato, Mexico by G. W. Uetz were maintained in a large plexiglass cage (91.0 L X 47.0 W X 35.5 H cm) located near a window to provide a natural photoperiod. This larger colony provided the "seed" individuals used for the experimental colonies. Temperature remained fairly constant at 28.8 ± 2.97 sd°C. Water was provided daily by a fine mist sprayed on the web surface; and animals were fed houseflies (*Musca domestica*) at weekly intervals.

Ninety one experimental colonies were housed in Petri dishes (52.2 cc) during the course of the study (8/22/81-1/28/82). Five group sizes were examined (N = 20, 10, 5, 2 or 1 adult females per container) to determine the effect of group size on colony activity and web structure. Direct observation and preliminary analyses of computer image data (see below) indicated that the rate of silk deposition levels off by day five of nest growth. For this reason, all data were collected from five-day-old experimental colonies. Previous data (Burgess 1979b, Jackson 1979, Tietjen 1982) indicate that *M. gregalis* is nocturnal. Data collection therefore began between 1500 and 1700 hrs, and experiments were terminated between 0630 and 0900 EST. Experimental colonies were fed houseflies (*M. domestica*) one day prior to their introduction to the arenas but were not fed during the five-day growth period. Had spiders been fed during this period, web structures would have been disrupted and measurements of nest complexity would not have been possible. Water was provided daily by depositing a drop near the edge of the Petri dish.

Buskirk (1981) indicates that coloniality in spiders may be related to high prey availability. Thus, the possibility exists that the spiders used in these series of experiments were stressed. Jackson (1980) maintained *M. gregalis* under conditions of starvation for as long as 53 days, and Witt (personal communication) maintained the spiders for four weeks without apparent ill effects. In a similar vein, Witt, Scarboro and Peakall (1978) used radioisotope techniques to determine the number of *M. gregalis* feeding on a single fly. Their data indicates that, even after 24 hr, none of their colonies had spiders that had all fed upon the prey. This minimal feeding level may be related to their low metabolic rate (88.0 ± 8.0 μl 0_2 /g body weight /hr); a value approximately ¼ that of *Araneus diadematus* (Witt, personal communication). Under field conditions, *M. gregalis* is likely to be presented with similar periods of high and low prey availability. Burgess (1979b) reports that the nests are sometimes surrounded by swarms of muscid flies, whereas prey availability at other times is so low that it can not be accurately measured. His results are consistent with the reports of Diguet (1909a, b) and Uetz (personal communication) who report that *M. gregalis* occupies a xeric habitat with fluctuations in prey availability. Although periods of high prey availability may have been important contributing factors in the evolution of sociality in *M. gregalis,* a predictable and consistently high abundance of prey is apparently not required for the maintenance of social behavior in this species under both laboratory and field conditions. For these reasons the short periods of low prey availability encountered in these series of experiments are not likely to affect the general conclusions of this paper.

Recording Methods.—Detailed descriptions of recording methodologies are provided elsewhere (Tietjen 1981, 1982). The system allowed for computer-assisted scanning of colony activity, occupation of space within the arena, and measurement of web structure and growth. In brief, a solid-state television camera (Periphicon Type 511), connected via a suitable interface to a CDP-1802 microprocessor-based computer, was located 0.65m above the experimental colony; and light was transmitted through the arena. The image in the camera's field of view was digitized into a 32 X 32 array providing 1024 picture elements (= pixels) which could potentially be occupied by the spiders and their web. Experimental arena shape reduced the usable recording area to about 620 pixels. Spiders appeared as black dots on a white background with each animal occupying a single pixel in the field of view.

The computer was programmed to record the occupation of space and activity of experimental colonies at approximately 30-sec intervals providing a total of 126,134 exposures. Occupation of space within the arena was recorded on a "map" of the arena in computer memory for each exposure. The number of moving spiders was determined by comparing sequential frames and recording the number of spiders moving from one frame to the next.

By transmitting light through the colony it was also possible to estimate the relative silk density at each pixel. High silk density areas (such as those associated with runways, reinforcement threads and silk-lined chambers) occluded more light than areas of low silk density. Thus, relative silk density and light intensity were inversely proportional. The relative silk density was recorded in 1024 levels of density for positions occupied by the colonies within the 32 x 32 grid. Blocks occupied by spiders or excreta were ignored in the silk density analyses by marking those pixels with the aid of a light pen. I compensated for possible nonlinearities in lighting intensity across the field of view by subtracting a optical density image of a control field from each of the silk density images.

Preliminary tests indicated that data (raw or transformed) did not fit parametric assumptions (Sokal and Rohlf 1969). All analyses were therefore nonparametric and were performed according to the methods of Conover (1971). Even so, all data are presented as the means and their standard deviations. Fourier analyses were based on the algorithm described by Owens (1981).

RESULTS

Web Structure.—*Mallos gregalis* readily built webs within the Petri dishes during the five-day growth period. These webs exhibited many of the structural features found in natural nests including chambers, silk runways and support

Table 1.—Effects of group size on web structure. Measures of web structure are presented in arbitrary units related to the optical density of the nest (see text).

Colony Size	Number of Colonies	Mean Silk Density	Maximum Web Density	Silk Deposition Per Spider
20	18	105.1 ± 13.7	375.0 ± 30.6	5.3 ± 0.7
10	17	78.1 ± 15.0	385.5 ± 30.6	7.8 ± 1.5
5	15	92.3 ± 11.9	305.3 ± 28.8	18.5 ± 2.4
2	20	45.3 ± 5.2	291.2 ± 60.6	22.7 ± 4.2
1	21	47.8 ± 4.2	205.0 ± 34.8	47.8 ± 4.2

threads (Tietjen 1985). The webs had their greatest silk density and structural complexity (i.e., chambers and tunnels) near the perimeter of the arena, with relatively simple, less dense sheets or silk-free areas found in the central parts of the arenas.

The mean silk density differed among groups, and was proportional to colony size (Spearman's rho ρ = + 0.35, $P<0.01$; Kruskal-Wallis Test Test, $P<0.001$; Table 1). The relationship between silk density and colony size was non-linear with the three larger colonies exhibiting equal mean silk densities. Silk density in these colonies was greater than, and significantly different from the two smaller groups (Mann-Whitney Test, $P<0.005$). Visual examination of the webs (Fig. 1) as well as quantitative indices of variation in silk density within nests (Maximum web density [Table 1], standard error and variance to mean ratios among blocks) indicated that the webs of the larger three colonies were more heterogeneous than the smaller two groups (Spearman's rho ρ = + 0.66, $P<0.0001$; Kruskal-Wallis Test Test, $P<0.001$). The high silk density areas were associated with chambers and tunnels in the web-interior, therefore variation in silk density is an index of nest structural complexity.

A qualitative estimate of the average silk deposition per spider was calculated by dividing the mean silk density of each web by the number of spiders in the colony (Table 1; Fig. 2). These data indicate that the mean silk deposition per spider is inversely proportional to colony size (Spearman's rho ρ = −0.86, $P<0.001$; Kruskal-Wallis Test, $P<0.001$).

Colony Activity.—Colony activity, recorded as the number of animals moving per minute, was somewhat proportional to group size (Table 2). The relationship was non-linear, however, with larger colonies exhibiting more activity than expected, and smaller groupings showing less than the expected activity (Spearman's rho ρ = + 0.69, $P<0.0001$; Chi-square, $P<0.001$).

An examination of individual colony activity indicated that activity in the larger groupings was not constant during the recording period, but rather was clumped into discrete periods of high and low colony movement (Fig. 3). To explore the possibility of periodicities in the behavior, the data were analyzed using a fast Fourier transform and spectrum analysis. A full statistical analysis of the power spectra (a measure of the relative "importance" of each frequency component) was not possible with the available equipment. For this reason, only the shortest significant period was recorded from the power spectra and compared among colonies (Table 2).

Neither of the two smaller groupings exhibited periodicities above the background noise (unresolved or nonsignificant periods) of the power curve, indicating the absence of significant short-term activity bouts during the recording

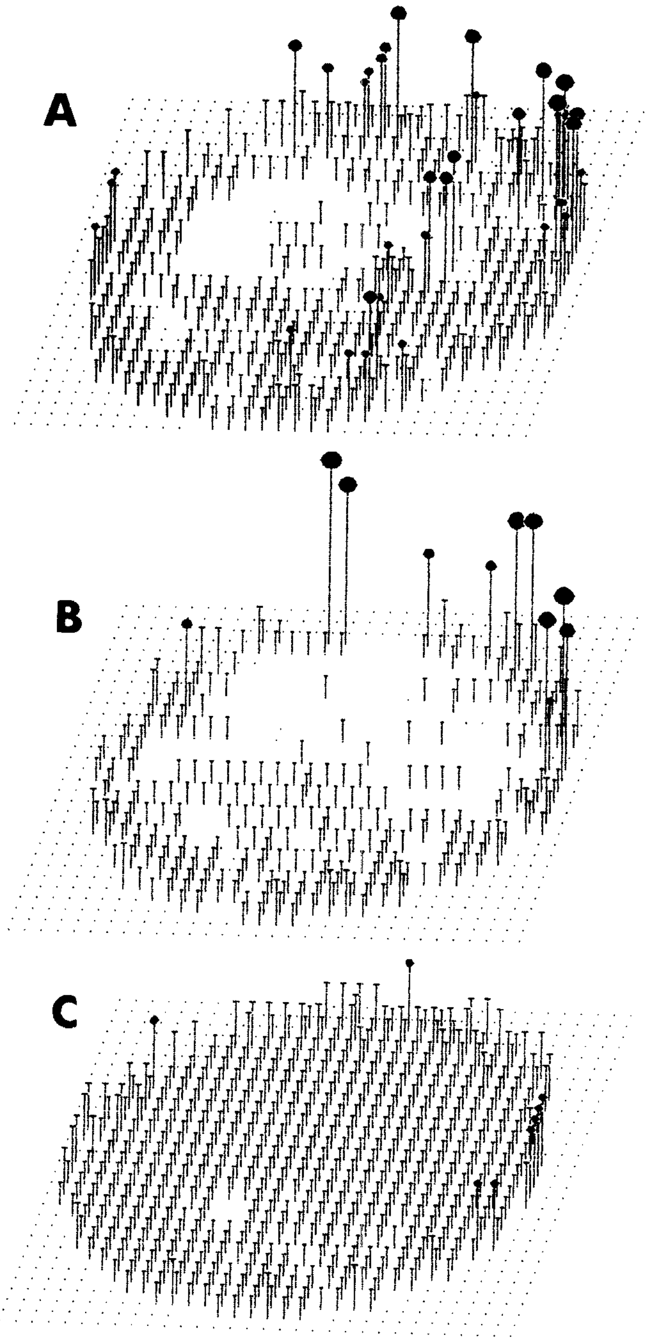

Fig. 1.—Effects of group size on relative silk density and structure. Representative silk density maps are provided for a) Colony size = 20; B) Colony size = 5 and C) Colony size = 1. Vertical bars represent relative silk density as determined by light transmission and displayed on a 0 to 10 scale which was optimized to display low density silk areas. The circles at the top of the bars provide additional cues as to the relative silk density; the larger circles representing denser areas of silk deposition (those blocks having chambers and tunnels). Small dots on the X/Y plane are areas located either outside the arena or blocks within the arena that were occupied by spiders or excreta. These blocks were ignored in the analyses. Note the silk-free areas in A and B and the extended low-density silk sheet in C. Also note the greater variation in web structure for the larger two colonies, and the concentration of silk near the edge of the arena. Experimental colonies of size ten were intermediate to those of size twenty and five. Groupings of size two were similar to those of size one.

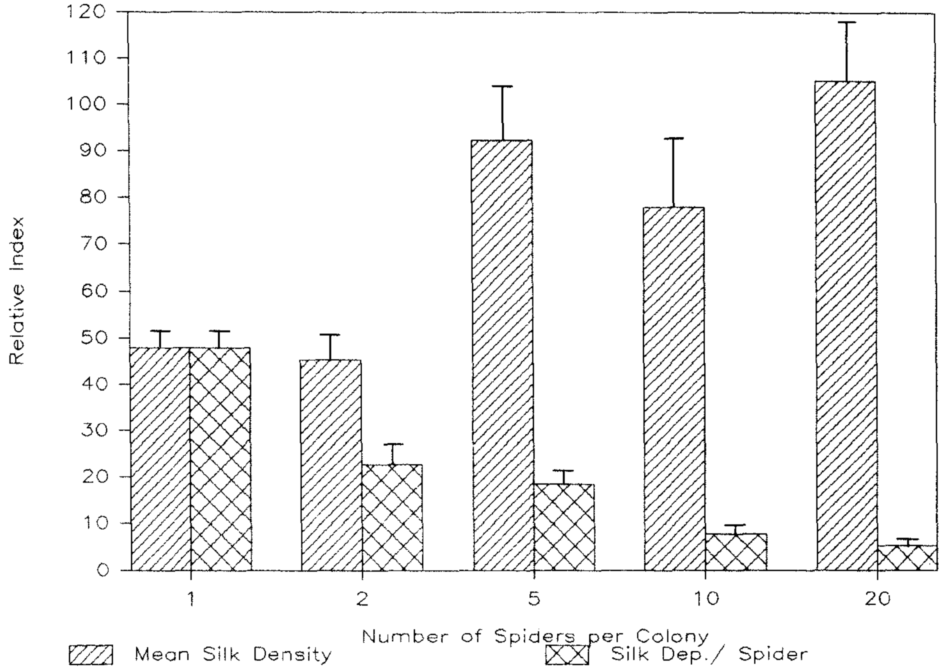

Fig. 2.—Effects of colony size on silk deposition. The relative index is an optical measure of silk deposition by colonies of size one-twenty. The mean silk density is presented as the averaged optical density of the colonies in arbitrary units. The silk deposition per spider is a qualitative index of the "work per spider" in building a nest.

period. Similarly, colony groupings of sizes five and twenty each had one sample with no significant periodicity while all of the remaining groups showed evidence of short-term periodicity. Examination of these remaining power spectra indicated that size-twenty colonies exhibited a shorter period than colonies of size five and ten (Spearman's rho $\rho = -0.36$, $P<0.05$; Kruskal-Wallis Test, $P<0.025$; Mann-Whitney Test, $P<0.01$). Colonies of size 20, for example, showed peaks in activity every 25.8 minutes whereas colonies of size five and ten had activity peaks separated by over 40 minutes.

The recordings of occupation of space within the arena indicated that, in general, spiders in all groupings mainly occupied the periphery of the arena, those areas characterized by the highest silk density and complexity (Fig. 4). Examination of these data also allowed the determination of two movement indices: an occupation index expressed as blocks occupied per hour per spider, and the percent inactivity. The first is an index of the space occupied by each spider, whereas the second is a measure of the number of runs (for each experimental group) which exhibited evidence of one (or more) animals showing no movement during the recording period (Table 2).

The percent of inactive spiders was inversely proportional to colony size (Spearman's rho $\rho = -0.82$, $P<0.0001$ Kruskal-Wallis Test, $P<0.001$). The occupation index varied directly with colony size (Spearman's rho $\rho = +0.50$, $P<0.01$; Kruskal-Wallis Test, $P<0.005$). Even among the larger colonies, however, the occupation index was below three blocks per hour per spider, indicating that most of the spiders' activity occurred within small areas of the web rather than on the entire web surface (Table 2).

Table 2.—Effects of group size on colony activity and occupation by *Mallos gregalis*. The coordination index is a measure of the shortest periodicity as determined by the Fourier analysis of colony activity. Indices of activity and occupation (blocks occupied per hour) are presented as means for each spider rather than colony means. Both the coordination index and maximum percent inactivity are colony means.

Colony Size	N	Activity Moves/min	Coordination Index (min)	Occupation Index	Maximum % Inactivity
20	11	0.35 ± 0.1	25.8 ± 4.4	2.0 ± 0.7	99.4 ± 1.5
10	10	0.33 ± 0.2	41.5 ± 4.0	2.6 ± 0.6	73.7 ± 27.5
5	10	0.22 ± 0.1	45.1 ± 8.3	1.8 ± 0.3	66.7 ± 22.2
2	12	0.16 ± 0.1	—	1.1 ± 0.2	80.9 ± 18.6
1	14	0.09 ± 0.1	—	0.5 ± 0.2	62.3 ± 35.8

DISCUSSION

Evaluation of Methodology.—The computer-camera apparatus was non-intrusive in the recording of animal position and activity and should have no effect on behavior. The peak sensitivity of the camera (900 nm wavelength) allowed monitoring using a light source which is outside the visual range of many animals, including spiders (DeVoe and Zvargulis 1967, DeVoe 1972).

The use of the computer-controlled camera necessitated confining the spiders within the limited area of a Petri dish. However, *Mallos gregalis* adapt well to such conditions and will construct functional webs in a variety of containers ranging in size from the arenas used in these series of experiments to room-sized environmental chambers. Nonetheless, animals so restricted exhibit apparently normal courtship, mating, prey-capture, and feeding behaviors over several generations (Tietjen 1980, 1986). In addition, by confining the animals to a relatively small and homogeneous area, intercolony variation for web structure within a treatment group is decreased, thus allowing for comparisons among groups using reasonable sample sizes.

The silk density analyses had a bias owing to the necessity of ignoring those blocks occupied by spiders or excreta. This bias, however, would tend to reduce web complexity estimates for the larger colonies, since spiders spent most of their time near the perimeter of the arena (which had the highest silk density). The error would have a greater effect on larger colonies, thus reducing their indices of silk density variation among pixels. In a similar manner, the removal of those blocks occupied by excreta would further reduce overall variability since most waste is deposited in the central part of the arena, that area utilized as the exterior of the web and having the lowest silk density estimates (Tietjen 1980). The two smaller groupings had most of their web surface composed of low-density silk, so ignoring excreta would tend to increase web variability. Thus, the bias in both cases tends to make the measures of web complexity and variability more conservative.

The delicate nature of the web and the availability of equipment made it impossible to correlate the silk density data with an actual quantity of silk at each pixel within the field of view. However, a visual comparison of silk density maps with actual colonies indicated that the silk density image provided an accurate sampling of high silk density sites, especially those associated with runways and chambers within the nest. For this reason, the variation in silk density within a colony is interpreted as a measure of web complexity. Those webs that were

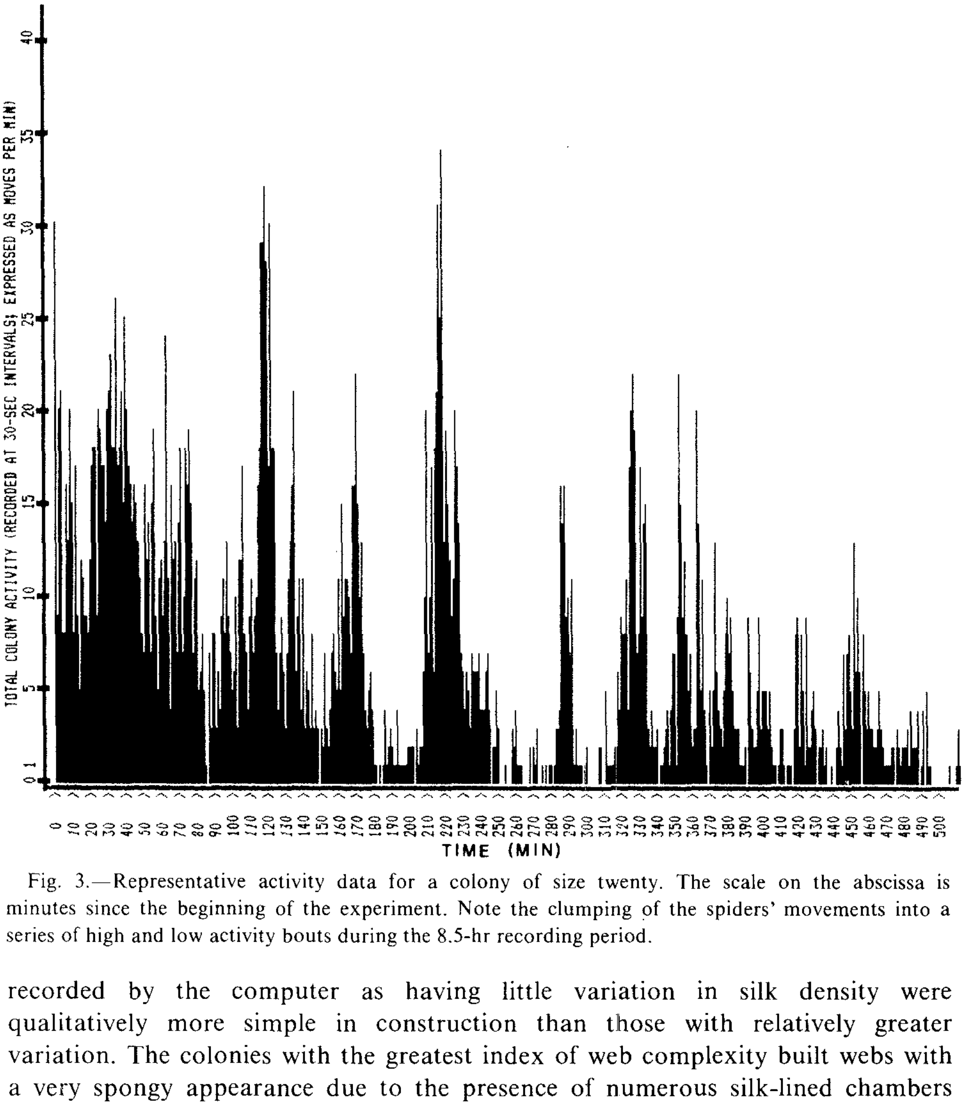

Fig. 3.—Representative activity data for a colony of size twenty. The scale on the abscissa is minutes since the beginning of the experiment. Note the clumping of the spiders' movements into a series of high and low activity bouts during the 8.5-hr recording period.

recorded by the computer as having little variation in silk density were qualitatively more simple in construction than those with relatively greater variation. The colonies with the greatest index of web complexity built webs with a very spongy appearance due to the presence of numerous silk-lined chambers and tunnels.

Web Structure as Related to Group Size.— Group size had a profound effect on the density and complexity of nest structure which extended beyond an arithmetic effect. Colonies of size 20, for example, did not simply deposit twice as much silk as colonies of size 10 since web density was not directly correlated with group size (the three larger colonies exhibited equal mean silk density). These data suggest that, for the larger groupings, a minimal amount of silk was required to support the construction of a nest which was to be occupied by several spiders. Similar results showing adaptation to group size (e.g. non-arithmetic changes in the behavior) are seen for web complexity, maximum silk density and the overall form of the nest.

Nests built by the larger groups had most of the silk concentrated at the edge of the arena. This outer section was characterized by greater structural complexity, including the presence of silk-lined chambers, runways and tunnels. The central portion of the arena had little or no silk, giving the larger nests a

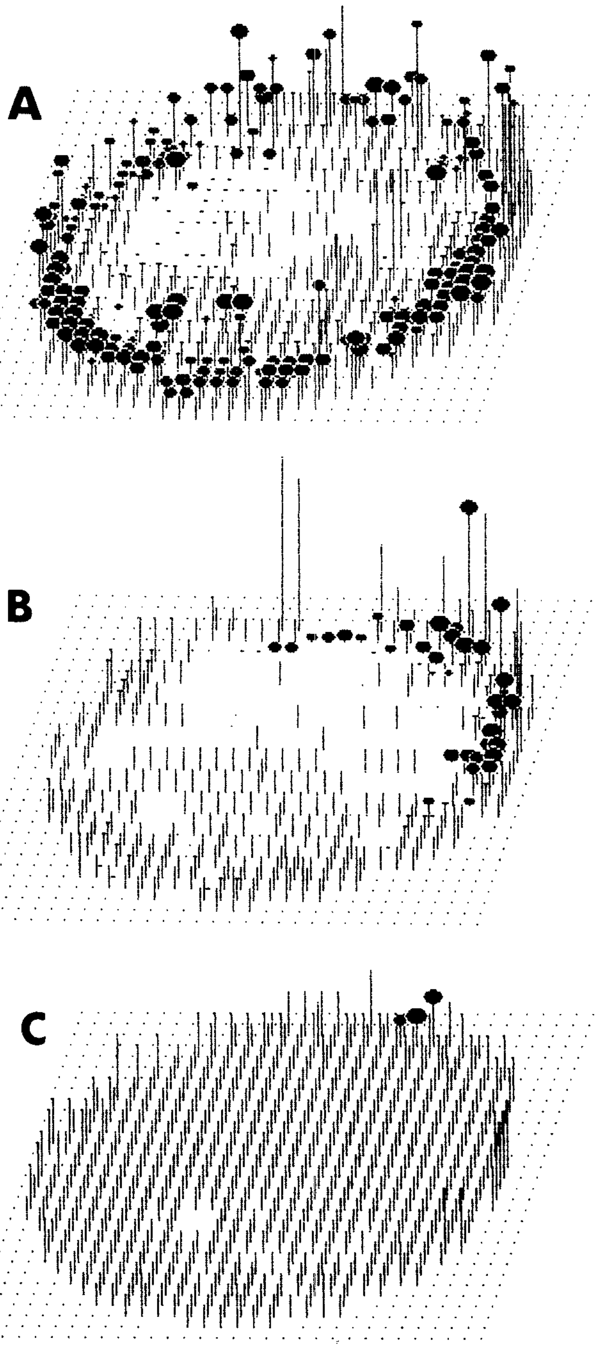

Fig. 4.—Effects of group size on occupation of space within the arenas. Three representative groupings are indicated: A) Colony size = 20; B) Colony size = 5 and C) Colony size = 1. As in Fig. 1, the vertical bars represent relative silk density. The circles at the top of the bars now indicate occupation of blocks within the arena. Those blocks that were most often occupied have the largest circles. Note the tendency for animals in each grouping to remain near the edge of the arena and the lack of long-distance movements by colonies of size one. Tests with groups of size ten were intermediate to those of size twenty and five. Groupings of size two were similar to those of size one.

toroidal distribution of webbing. The greater density of silk near the periphery was largely responsible for the increase in mean silk density with respect to group size. In contrast, webs built by groupings of one or two spiders were far less complex in construction, having few silk-lined retreats, and no runways or tunnels. In addition, a finely spun silk sheet extended through the central portion of the arena. Such sheets of silk were characteristic only of those webs built by the smaller groups.

The greater silk density and complexity produced by the three larger groupings would allow these colonies greater potential for exploitation of marginal habitats. In the laboratory and field, groups of *M. gregalis* roll or tie together leaves of the supporting foliage and construct a prey capture sheet on the surface of the plant, a process which does not kill the underlying foliage. Within the interior of these nests, the spiders build chambers and tunnels between the leaves. Individual spiders do not build such structures under laboratory conditions, but rather confine their building of a prey capture sheet to the surface of adjacent leaves. By taking advantage of the structure provided by the supporting foliage, the larger colonies would be afforded protection from sun, wind and rain, while allowing *M. gregalis* to take advantage of leaf transpiration to cool the nest (Tietjen 1986). In addition, a more dense and complex web would be expected to provide greater protection from potential vertebrate predators (Buskirk 1981, Rypstra 1979, Tietjen 1986). The web structure of the smaller test groupings lacked the complexity seen in the larger groupings. most of the nests built by the smaller groupings had only one or two silken chambers which could be used as retreats. These nests are qualitatively similar to webs built by solitary dictynids (Chamberlin and Gertsch 1953, Kaston 1948). Even among those groupings having two members, the structure of the web was more similar to that seen in solitary species than to social ones. This suggests that *M. gregalis* is capable of shifting web-building behavior from a communal-cooperative mode of construction to a solitary mode of behavior.

Under unrestrained conditions in the laboratory, individual *M. gregalis* may leave the parent colony and build single-spider webs. Spiders occupying such webs usually remained isolated from the original colony and were competent in prey-capture behavior. These data, in conjunction with the quantitative differences observed in the structure of the nests between the large and small groupings, suggest that *M. gregalis* is, to some extent, a facultatively-social spider.

The silk deposition per spider was inversely proportional to colony size. Although these data do not represent the actual metabolic expenditures for individuals, it is reasonable to assume that the differences observed among the groups do reflect varying physiological burdens. If this is so, the data indicate that another advantage of cooperative nest construction is a decrease in energy expenditure per individual spider. A more complete explanation of this effect will require an analysis of the caloric content of webs built by groups of differing size.

Colony Activity as Related to Group Size.—Measures of mean activity per spider, patterning of activity bouts and occupation of space within the arena were also affected by group size. As was the case for web structure, the changes observed for each of these behaviors extended beyond an arithmetic effect and instead represent shifts in the behavior of *M. gregalis* with changes in colony density.

The data indicate that the mean activity of individuals in larger colonies was greater than that of the smaller, with members of the largest two colonies being-three to four times more active than isolates. This evidence, taken alone, might indicate that a major disadvantage of group-living in *M. gregalis* is an increase in metabolic costs due to greater activity. However, most of the activity observed in the larger colonies was short-distance movements and turning in place as shown by the mean number of blocks traversed per hour per spider, this translates to an actual distance of less than 8mm per hour as compared to a distance of 2-4mm per hour for the smaller colonies. Thus, although the movement indices of the larger colonies are higher than those seen in smaller groupings, the actual metabolic cost of the activity is likely to be low. It is possible that greater efficiency in nest construction (e.g., work per spider) more than offsets the slight increase in activity seen among the larger colonies. nearly 100% of the larger colonies had animals which did not move during the recording period whereas smaller groupings exhibited less total inactivity (Table 2). This suggests that in larger groupings, individuals may have greater opportunity for extended periods of inactivity since they do not have to expend as much time in nest construction. The Fourier analyses indicated that the larger colonies organized their nocturnal rhythms into a series of high-activity bouts. Colonies of size 20 showed greater coordination in the patterning of activity bouts as evidenced by their shorter periodicity as compared to the smaller groupings.

The proximate cause for the patterning of activity seen in the larger groupings is most likely due to web-transmitted vibrations. Thus the vibrations caused by the movements of a single spider could induce movement in other colony members. Similar effects have been described in several social species including *Cyrtophora citricola* (Rypstra 1979), *Metepeira spinipes* (Uetz, in press), and *Oecobius civitas* (Burgess 1976).

Vibrations transmitted through the web by walking spiders are extended below the response window of 30-700 Hz recorded by Burgess (1979a), who suggested that the movements of spiders are damped whereas vibrations of struggling prey are enhanced. Although it is clear from Burgess' work that fly vibrations are accented by the web structure, the potential for low frequency vibrational communication among nest mates is still possible for *M. gregalis.* Hollar (in Tietjen 1986) used a more sensitive photo-optic transducer than was available to Burgess to record web movements and demonstrated that the vibrations of normally walking spiders can be transmitted over distances of 10 cm or more. Similarly, Jackson (1978) reports that the courtship vibrations of male *M. gregalis* occur at about 10 Hz. These data suggest that the vibrations caused by the movements of spiders could provide a means of intra-colony communication.

The occupation index and an examination of the space-utilization figures indicate that members of the larger colonies occupy a greater area within the Petri dishes than do those of the smaller groupings. Examination of the space-utilization figures indicates that nearly all of the recorded activity was short-distance movements (probably turning in place, silk depositions and grooming movements). If the cribellate silk lining of chambers dampens the vibrations caused by the movements of other spiders on the web, then animals located within these structures could effectively remove themselves from the stimulation caused by the activities of their nestmates. Casual observations suggest that animals located outside chambers are more responsive to the movements of other spiders on the web than are those located within chambers. Thus, the structure of the chambers could allow a proportion of the colony to maintain an in active state without being stimulated to active behavior by the movement of other colony members, as suggested by Tietjen (1982).

The organization of colony behavior among the Araneae does not depend on coordination provided through ethological or morphological caste systems but rather on mass action behavior, chemical communication, vibratory signals, and periodicities in activity and occupation of web sites (Tietjen 1986). Web-transmitted vibrations and interindividual interactions during activity peaks could provide an efficient means for individuals to ascertain current colony conditions related to population density and colony reproductive state. These effects, coupled with web-position dependent behaviors, and chemical communication may aid in organizing colony behavior.

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