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**GENETIC DIFFERENCES IN SOCIAL BEHAVIOR AND
SPACING IN POPULATIONS OF *METEPEIRA SPINIPES*,
A COMMUNAL-TERRITORIAL ORB WEAVER
(ARANEAE, ARANEIDAE)¹**

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ABSTRACT

Metepeira spinipes F. O. Pickard-Cambridge, a communal/territorial orb-weaver from Mexico, shows considerable geographic variation and temporal flexibility in spacing. A series of laboratory studies was conducted to test whether the variation in spacing observed in the field is solely the result of behavioral plasticity in response to environmental conditions, or the result of mechanisms inherent in different populations (i.e., genetic differences in behavior). Spiders from source populations in desert and moist tropical habitats were collected as eggs and raised in the laboratory under identical controlled conditions. Measurements of three-dimensional spacing parameters in laboratory colonies (nearest neighbor distance, within-colony density) have shown significant differences in spatial organization between populations, suggesting a genetic basis to these differences. Behavioral observations confirm that there are behavioral ecotypes within this species, with levels of sociality adapted to the regions in which they occur.

INTRODUCTION

There are constraints on the social behavior of orb weaving spiders (families Araneidae and Uloboridae) that make the evolution of sociality less likely in this group. Unlike the sheet or tangle webbing of spiders in other families which exhibit communal web building (Theridiidae, Agelenidae, Dictynidae, Eresidae, Amaurobiidae, Oecobiidae, Pholcidae), the orb web cannot be built by more than one spider. It is the result of a complex sequence of behaviors which are tightly controlled by the genetic "program" of individual spiders (Witt and Reed 1965, Witt et al. 1968), unlikely to be modified to include participation by others (Lubin 1974, Burgess and Cangialosi 1982). Thus, cooperative web construction, at least of the prey catching portions of the web, is precluded.

Most orb weavers are limited in their social organization to aggregations of potentially of potentially competing individuals building and occupying their own webs within a shared web foundation (Lubin 1974, Buskirk 1975, a,b, Fowler and Diehl 1978, Uetz et al. 1982, Smith 1983). This type of social organization is termed "communal/territorial" (Jackson 1978), and is conceptually (and

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sometimes evolutionarily) intermediate between the incipient sociality of fortuitous spider aggregations, and more advanced social spiders (which exhibit cooperation in prey capture, feeding, and brood care) (Buskirk 1981, Burgess and Uetz 1982, Rypstra 1983).

These spiders must reconcile the demands of conflicting behavioral strategies—communal aggregation and defense of space—while at the same time contend with a mosaic of contiguous territories in three dimensions instead of two. The result is a three-dimensional spatial arrangement of group members which is somewhat fixed, yet may change every time webs are renewed (usually on a daily basis) depending on the outcome of aggressive interactions between individuals. The “territory” defended has indistinct boundaries, in that the silk connections between the retreat, the orb or catching spiral, and the space web are connected to and overlap with these of other individuals. In addition, this is a “multipurpose territory” (Davies 1978), in that it may include a foraging site (the orb), a habitation (the retreat), a mating site (orb and/or retreat), and a breeding/egg laying site (the retreat). Thus, the spatial organization of communal/territorial orb weavers reflects a compromise solution to the conflicting selection pressures of competition for space and food resources and for benefits gained from communal foraging. An analysis of spatial organization in these spiders should clarify the relative importance of those selection pressures in the evolution of spider sociality.

For several years, we have studied the behavior and ecology of *Metepeira spinipes* F. O. Pickard-Cambridge (Araneidae), a communal/territorial orb-weaving spider species found in central Mexico (F. O. Pickard-Cambridge 1903). Previous studies have shown considerable between-population variation in the spatial organization of this species (Burgess and Uetz et al. 1982, Uetz 1983, Uetz et al., in press). This variation makes *M. spinipes* an interesting species with which to investigate spacing, and raises questions about the influences of environmental and genetic factors on the social organization of communal-territorial spiders.

BACKGROUND

Metepeira spinipes occurs solitarily, but more frequently occurs in groups of 5 to 150 or more individuals (Burgess and Witt 1976, Uetz and Burgess 1979). *Metepeira spinipes* is the only communal species in this genus (Levi 1977), although there is one other species, *Metepeira daytona* Chamberlin and Ivie, found in the Carribean, which occasionally exhibits group web-building (Schoener and Toft 1983). The genitalia of all specimens examined to date resemble the drawings of Pickard-Cambridge in the species description. In addition, preliminary studies of genetic differentiation between populations in different geographic areas using starch gel electrophoresis tentatively indicate that *M. spinipes* is a single species (Uetz et al., in press).

The web of individual *Metepeira spinipes* (Fig. 1) contains a three-dimensional space (or barrier) web with a retreat, and a sticky orb connected to the retreat by signal threads (Burgess and Witt 1976). Although the sticky orb webs are taken down and renewed on a daily basis, a communal space web persists and acts as a framework for the web building activities of numerous individuals. The



Fig. 1.—Schematic diagram of a colony of *Metepeira spinipes*.

resultant 3-dimensional colony consists of spiders inhabiting interconnected, fixed, foraging locations, potentially changing positions on a daily basis. Individuals maintain and defend orbs and retreats within the colony, and capture their own prey.

Group size in *M. spinipes* varies with habitat (Uetz et al. 1982). In severe habitats where prey availability is low (e.g. desert grasslands), spiders are predominantly solitary or live in small groups. In sites where climate is benign all year and insect abundance is great (e.g. moist tropical forest), colony size is very large. Nearest neighbor distance decreases over the habitat gradient between these sites and in general appears to be inversely related to prey availability (Uetz et al. 1982, Uetz et al. in press). This relationship is further supported by the results of field experiments, in which nearest neighbor distance increased in colonies after relocation to prey-poor sites, except when colonies had prey supplemented (by addition of cow dung to their new sites) (Uetz et al. 1982).

Metepeira spinipes can apparently tolerate conspecifics at closer distances in areas where prey are more abundant, as Riechert (1978a) has found in *Agelenopsis aperta* (Gertsch), a solitary, desert funnel web spider. *Agelenopsis* has a minimum territory size, genetically set at an area that provides the spider with sufficient prey biomass (Riechert 1981, Riechert in press). In contrast, *M. spinipes* shows a rapid change in spacing when food availability changes. This may be explained by the fact that orb weavers, unlike funnel web builders, renew their web on a daily basis (Uetz 1985, Riechert and Gillespie, in press). In this communal/territorial orb weaver, rising hunger and aggression levels associated with food deprivation may result in greater nearest neighbor distances when the webs are rebuilt each day.

Observation of behavior and spacing patterns of spiders in laboratory cages confirm the findings of field studies. Spiders in cages at low levels of prey

availability were spaced at significantly greater distances from each other than those in cages at maintenance or satiation levels of prey (Uetz et al. in press). Instances of cannibalism ($n = 9$) were highest in the low prey availability cages (30%), and very low (3%) in the other treatments. There were no significant differences in nearest neighbor distances of spiders at maintenance and satiation levels of prey. This suggests that there is an intrinsic lower limit of distance (analogous to territory size) at which conspecifics can be tolerated.

Genetic differences in the degree of tolerance of conspecifics are suggested by laboratory observations of differences in the behavior of field collected *M. spinipes* from various localities. In particular, spiders from the tropical site appear far more tolerant of each other. During transport, many individuals can be placed together in small containers with water but no food, and survive for up to two weeks without cannibalism. In contrast, spiders from the other populations cannot exist under these conditions for more than a day or two. In laboratory cages under identical conditions, field collected individuals from the tropical site and desert site show distinct differences in web building behavior, web structure, and inter-individual spacing. These differences are apparent from the first day of introduction to the cages (Uetz et al. in press).

The questions raised by the results of these earlier studies concern the possibility of some genetic control of social organization in this species. Could the very wide range of group size and spacing seen in *M. spinipes* be solely the result of behavioral plasticity in response to climate and food availability? Or, is it possible that different social behavior or tolerance strategies are selected for in different environments and are reflected in the differences seen between populations? To answer this question, an experimental study was conducted in the laboratory using a classic behavior genetics technique—rearing spiders from different populations under identical, controlled conditions.

In this study, most proximal environmental (ecological) factors that might influence spacing in *M. spinipes* (climate, predation, availability of prey, web site availability, colony density) were controlled in the laboratory. Thus, differences in nearest neighbor distance and other spacing parameters between populations that might be attributable to genetic factors inherent in the populations can be revealed. Experiential factors, and the interaction of genes and environment are investigated in another study (Cangialosi and Uetz, in prep.)

METHODS

Representative field sites were chosen in three geographic regions where populations of *M. spinipes* exhibit different levels of social behavior as indicated by group size and spacing: (1) In the northern desert region, near San Miguel de Allende, where *M. spinipes* is found in small groups with maximal inter-individual distances. (2) In the tropical mountainside of Fortin de las Flores, where the spiders are found in very large groups with minimal inter-individual distances. (3) In the central valley of Mexico, in Tepetzotlan, an agricultural area north of Mexico City, where the spiders are found in group sizes and with spatial organization intermediate between (1) and (2) above. These sites represent the range of variation in social spacing seen in this species, and are easily accessible, being located off major highways. The vegetation and environments of these areas

are described in Shelford (1963) and previous data on climate variables, prey insect availability, and aspects of *M. spinipes* natural history are also available (Uetz et al. 1982, Uetz 1985, Benton and Uetz in press).

Egg sacs were collected from the field sites in October 1982 and February 1983 and brought back to Cincinnati, Ohio for laboratory rearing under controlled environmental conditions. Spiderlings used in the experiment were selected from several egg sacs or egg sac strings. Each experimental group was a mixture of eggs from six females, taken from different colonies of equal size at each site, in order to minimize (or at least equalize) possible maternal effects. It is certainly impossible to control for all differences between eggs, especially when collecting them from females in the field (whose precise individual history is not known). However, they were collected from sites (and in some cases, colonies) for which previous ecological data are available, and this selection process undoubtedly reduced the potential for error between experimental groups due to egg differences within each group.

Spiders were housed in a walk-in environment room with light regulated on the same daily regime occurring in their natural habitat (12 hrs light; 12 hrs dark). Spiders were raised to adulthood under conditions of controlled climate (Temperature 27°C; Rel. Humidity 75%). These conditions are optimal for survival of *M. spinipes*, as established from previous research.

Spiders were raised communally through adulthood in groups of 30 individuals in cages (100 cm X 75cm X 80 cm) where cultures of *Drosophila* and *Musca* flies provided prey ad libitum. Three cages of spiders from each population (desert and moist tropical forest) were established. Spiders were supplied with prey ad libitum in order to control for hunger as an influence on spacing. Under conditions of apparent food satiation, a minimal interindividual spacing level is reached (Uetz et al. in press). In a separate study (Cangialosi and Uetz, in prep.) spiders were reared individually in isolation to control for experiential effects.

The fixed colony size (30 spiders per cage) for this experiment was arrived at after many attempts at rearing these animals at a variety of densities, and was chosen for several important reasons. First, by keeping the number of spiders constant in all cages, differences in spacing seen in the field due to the compound influence of population density and dispersion are eliminated. Second, it is important not to set up a false test of spacing differences—where spiders from the desert are overcrowded, experiencing a density far greater than they would in nature, while the tropical spiders spread out their webs in what to them may be wide open space. Having 30 spiders in a cage yields a group size in the upper range for the desert spiders (yet still encountered in nature with a frequency 0.05), and a density of approximately 40 spiders/cubic meter (which is by no means overcrowded—densities far greater are seen frequently in nature). Likewise, this group size and density are not unlike those seen for smaller colonies in the tropical population under natural conditions.

The chosen colony size also serves as a conservative test of the tendency for individuals from the tropical population to be spaced closer together, even when space is not limiting. If inter-individual spacing expands, then it may be assumed that in nature, some aspect of colony size and density (e.g., intrusion by other spiders on individual space), is causing spiders to be spaced more closely together (Hixon, 1980, Schoener 1983). If cages housing individuals representing tropical populations show smaller nearest-neighbor distances (NND) than cages with

spiders from desert populations (as has been observed in previous studies), then an inherent tendency toward closer association with conspecifics will be demonstrated.

Using a fixed number of spiders per cage raises another set of problems that must be addressed—what happens if there is differential mortality in cages? Might this differentially affect nearest neighbor distance? As luck or fate may have it, there was some mortality, but statistical analysis has shown that there is no apparent directionality in its effect; NND and subsequent no. of spiders/ cage are not significantly correlated for all cages from both populations ($r = 0.21$; $p > 0.45$).

Each of the cages was gridded with cm markers on the outside, so that the exact position of each animal within the group could be determined using x, y, z coordinates. Positions of individuals within colony cages were recorded at regular intervals corresponding to developmental stages (immatures: instars 5-7; pre-reproductive adults, reproductive adults), using the aforementioned coordinates. This was done to insure that when measurements were taken, all spiders (from both populations) were at approximately the same stage and size, reflecting equivalent territory sizes. Data collected on location of individuals within colonies were loaded into a computer program used to calculate nearest neighbor distances using the following formula (Buskirk and Uetz 1982, Major and Dill 1978):

$$\text{Distance (1, 2)} = [(X_2 - X_1)^2 + (Y_2 - Y_1)^2 + (Z_2 - Z_1)^2]^{1/2}$$

Distance between all possible pairs of animals may be obtained using this formula, and the computer program calculates means for 1st, 2nd, 3rd...Nth nearest neighbors. Nearest neighbor distance is a widely used measure of animal spacing, and provides a means of quantitatively comparing populations.

Density of spiders within the colony was also calculated. Because the number of spiders per cage remains fairly equal between cages, this measure estimates the internal cohesiveness of individual spacing within the group. A direct measure of density was used by determining the amount of the cage occupied by the communal web, and dividing that into the number of spiders per cage. Thus, if there was any mortality, the measure of density was scaled by the size of the spider colony and not nearest neighbor distance (as in other measures).

Spiders were observed in cages between 6:00 AM and 9:00 AM EST, which is the time period during which webs are built and most behavioral interactions occur (3 hours before "dawn"). A total of 9.5 hours observation time for the desert population, and 8.25 hours of observation time for the tropical population were accumulated in short periods (approximately 30 minutes—1 hr at a time) over several weeks. Numbers of interactions were totalled for each population, and sequences of behavior during each interaction were recorded.

In Fortin de las Flores in August 1983, positions of nearest neighbors relative to each other in 3-dimensional space were examined within a small colony (approx. 100 individuals) and a much larger one (approx. 1500-2000 individuals), determined from location data in both horizontal and vertical aspects. Orientation of individuals facing webs (and thus the direction the web faces) was recorded in xy plane, and set as zero degrees. Location of individuals relative to each other in the xy plane (bearing) and in the xz plane (elevation) was recorded with the vertical axis set at zero degrees.

Table 1.—ANOVA: Nearest neighbor distances of spiders in laboratory cages (* = < 0.05).

Time Period	Development Stage	Source of Variation	F Value
1	immatures (instars 5-7)	Source Population	17.43*
		Replicates	1.38
2	penultimate	Source Population	8.85*
		Replicates	2.53
3	pre-reproductive adult	Source Population	24.64*
		Replicates	4.84
4	reproductive adult	Source Population	35.74*
		Replicates	0.60
5	adult females with eggs	Source Population	7.28*
		Replicates	1.20

RESULTS AND DISCUSSION

In the laboratory, under identical controlled conditions, significant differences were seen in the spacing of spiders from separate source populations at all stages of their juvenile development (Table 1). The spiders from the moist tropical site in Fortin de las Flores had a significantly lower nearest neighbor distance (NND) than spiders from Tepetzotlan or San Miguel de Allende (Duncan's Multiple Range Test, $p < 0.05$). Spiders from the desert grassland population (San Miguel) and the agricultural central valley (Tepetzotlan) showed no significant differences in NND.

NND actually varies very little over several months' time in the laboratory (Figure 2), which suggests that under these conditions, the spiders maintained a minimum NND. This suggestion is supported by a comparison of field and lab data for adult females. In populations from San Miguel and Tepetzotlan, lab NND was significantly lower than field NND (Student's "t" test with unequal variance correction, $p < 0.05$). For the populations from Fortin de las Flores, no difference was seen in lab and field NND, perhaps because prey are so abundant in the field there. At that site, however, female—female distances may be misleading, because all ages are present at one time. In the lab, cohorts of similar ages comprise the colonies.

An early concern in this study was that random mortality might cause the numbers of spiders in each cage to be different, and thus influence NND. However, within each time period or set of cages, NND and number of spiders per cage (after mortality) were not correlated (Person's "r" = 0.21; $p < 0.45$). Even so, to guard against such a possibility, a measure of spacing independent of NND was made by estimating the density within colonies (no. of spiders/m³) by measuring the volume of the webbing and dividing it into the number of spiders in the cage. A comparison of the observed density and the expected density (based on the no. of spiders/volume of cage) (Figure 3) shows a significant difference between spiders from the moist tropical site and those from the other two areas (G test; $p < 0.01$). These data suggested that spatial arrangements within colonies differ between populations, and in fact, consistent differences in the spatial organization within colonies were revealed. When actual positions of spiders were plotted in three dimensional graphic arrays, spiders from Fortin tended to group in a cluster in the upper center of the cage, whereas

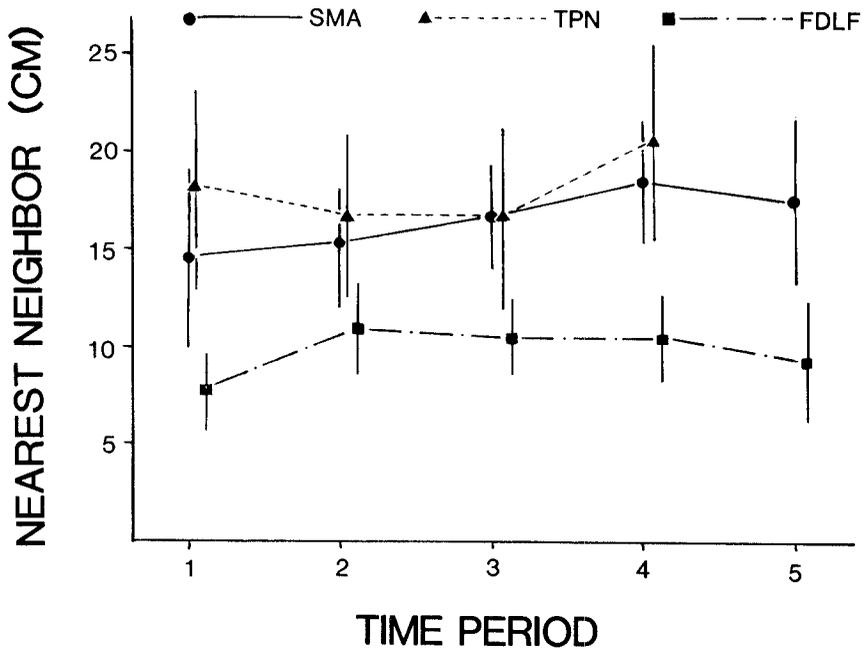


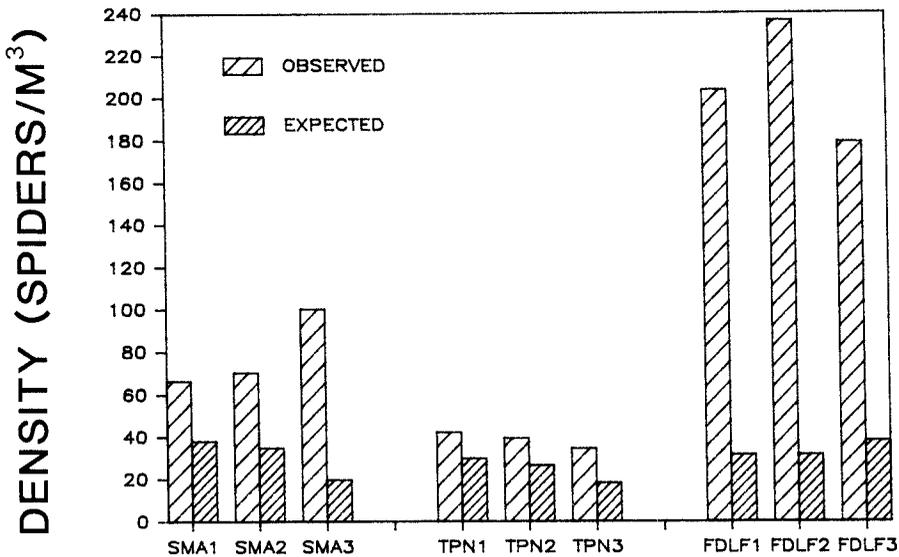
Fig. 2.—Mean nearest neighbor distance \pm 95% conf. limits) of three replicate *M. spinipes* colonies, each set from three different field populations and reared over their life cycle in the laboratory under identical conditions. (SMA = San Miguel de Allende; TPN = Tepetzotlan; FDLF = Fortin de las Flores). Time periods represent developmental stages as indicated in text and Table I.

spiders from Tepetzotlan and San Miguel tended to be dispersed throughout the cage (Fig. 4a, b). These differences were consistent in all cages, and throughout all time periods.

From these findings, it is apparent that populations from the extreme ends of the range of spacing seen in nature show consistent differences in NND when raised under identical conditions (conditions which should result in a minimal level of distance between neighbors). Although the remote possibility of some maternal or egg effect cannot be ruled out entirely, these data suggest some genetic differences, perhaps influencing behavior and thus spacing. It is probable that there are ecotypes (genetically distinct subpopulations), subspecies, or emerging species populations showing differences with respect to social behavior, which have spacing arrangements adapted to environments where they occur. Genetic influences, acting along with environmental influences like climate and food availability, result in the variation in social spacing observed in earlier studies.

An important question that must now be raised concerns the nature of genetic control of spacing behavior. How can genes influence the nearest neighbor distance in a colony of spiders? There would appear to be two main ways in which this could occur, and there are several lines of evidence supporting each mechanism.

It may be possible that there are differences in the interaction strategies of spiders that have become genetically fixed in each population (as has been found for *Agelenopsis* by Riechert 1983, 1984) resulting in clear differences in the levels of aggression shown. More aggressive spiders would be widely spaced, whereas



SOURCE POPULATION

Fig. 3.—Density of *M. spinipes* in laboratory colonies (see text for explanation of observed and expected values).

less aggressive ones would be spaced closer together. Spiders from the desert and moist tropical forest populations, maintained in laboratory cages under identical controlled conditions of this study, show differences in their interactive behavior. In 9.5 hours of observation, spiders from the desert population had 40 encounters in which agonistic behavior was seen (0.178/spider-hr). In contrast, in 8.25 hours of observations, the spiders from the tropical forest population had 119 such encounters (0.560/spider-hr). This apparent difference would at first appear counter to both theory and previous findings. An explanation may be found in the actual patterns of behavior seen in these interactions (Figs. 5a, b). In the tropical population, where agonistic encounters are more frequent, a majority of bouts are concluded with a single web pluck exchange (Fig. 5a). In the desert population, bouts are more prolonged, and escalate more quickly to chasing and grappling (Fig. 5b).

These findings are consistent with the predictions of game theory, as demonstrated by Riechert (1982, 1983). Selection would favor an aggressive behavior strategy that is appropriate for the level of resource availability in the local environment. If space and food were the limiting factors, an aggressive behavior strategy which results in the securing of a web site within the colony at the optimum level of cost/benefit would prevail. For the desert population, where web sites and food availability are limited, a strategy of rigorous defense of territory is appropriate. In tropical colonies, where prey are abundant and the quality of web sites within the immense communal web may be more or less equal, the appropriate strategy is for intruders to give up without a fight, and move elsewhere. This may also be true of residents, which have often been observed giving up a web to a more persistent intruder. The outcome of these different strategies is that once settled into web locations, desert spiders move

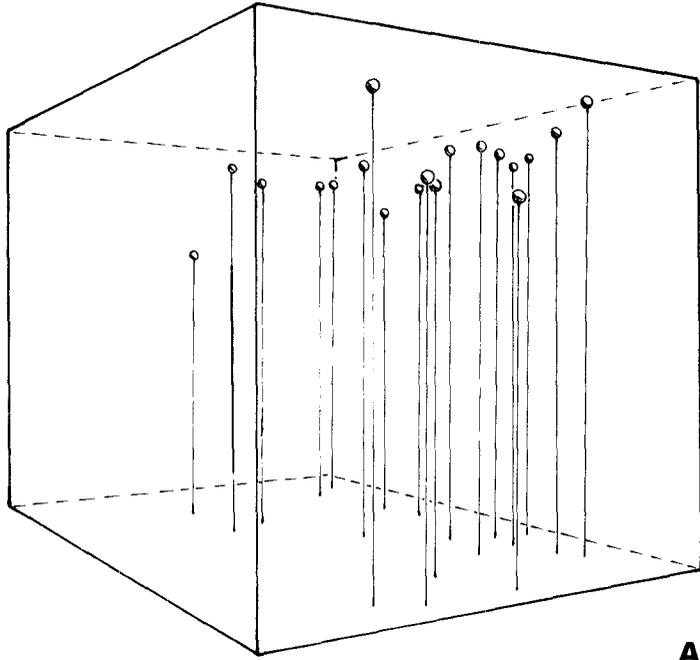
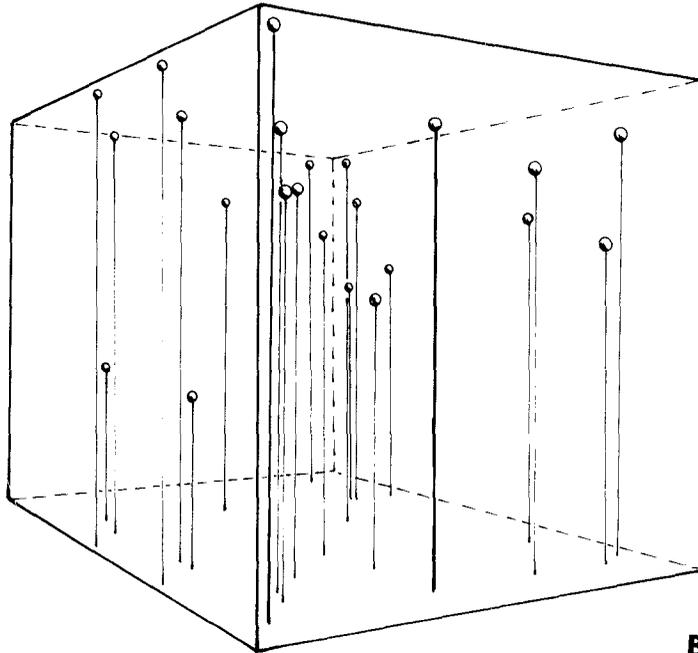
**A****B**

Fig. 4.—Location of individual spiders in laboratory colony cages (a) a representative FDLF cage; (b) a representative SMA cage.

considerably less often than tropical spiders do, and thus fewer aggressive encounters occur among them.

It may also be possible that there is a fixed distance at which an intruder on the web "territory" will be met with aggressive behavior, and that this distance varies between populations. The result would be that some populations of spiders are inherently more tolerant of neighbors at closer distances, and would be spaced more closely than others. In communal/territorial web building spiders, the location of nearest neighbors in space, and the orientation of their webs may relate to competition among colony members, or may somehow relate to prey capture success. Observations of encounters between spiders suggest that the presence of an intruder at some point close to the retreat or web will result in the initiation of agonistic behavior sequences. We have observed that the location of the intruder relative to the resident at the time this conflict is initiated varies, which may provide some support for the concept of a variable, 3-dimensional "territory" in these spiders. Differences in territory size between populations might be determined by whatever minimum area is required to provide an individual with sufficient prey, based on its availability in the habitat, as has been shown for *Agelenopsis* by Riechert (1978).

Field studies of spiders from the tropical population have shown that the location of nearest neighbors and the orientation of their webs relative to each other changes with colony size. In these studies, nearest neighbor location data were plotted in hemispheric projection relative to a central point by making the reference individual the one whose nearest neighbor is measured. This type of projection (Fig. 6a, b) was used in order to determine any patterns in nearest neighbor spacing (as in Major and Dill 1978). This also allows a determination of the basic shape of the 3-dimensional territory. As colony size increases, spiders become more tightly packed, with webs facing opposite directions, and a pattern emerges (Fig. 6b) wherein nearest neighbors are located behind and below, or to the side of a spider's web (but never above or below in front of the web). This suggests that territorial space within the colony is asymmetrical and compressible, and that spiders are more tolerant of neighbors in locations where they pose less of a threat to obtaining food. Data are not available for the desert population, but it is possible that the size, shape and degree of compressibility of this 3-dimensional territory may differ there.

The differences in social behavior observed, as well as morphological differences between populations, might indicate that *Metepeira spinipes* is not a single species. There are consistent size differences, and spiders from Fortin are smaller and have shorter legs than spiders from the other populations. There are also consistent differences in the abdominal folium and ventral markings. However, specimens show considerable individual variation (including those from the same colony), and look slightly different, presumably because the flexible scape of the epigynum preserves at varying orientations, and the degree of abdomen distention affects color. Research on genetic similarity of *M. spinipes* populations from these and several other areas in Mexico using polyacridamide gel electrophoresis, has shown all populations to be highly similar. Nei's Index of Similarity (Nei 1972) for these populations was > 0.96 (Uetz et al., in press), a level of genetic similarity in the range of variation seen within many arthropod species populations (Selander and Johnson 1973, Ayala 1976). These studies, however, were done comparing only a few loci within a limited number of

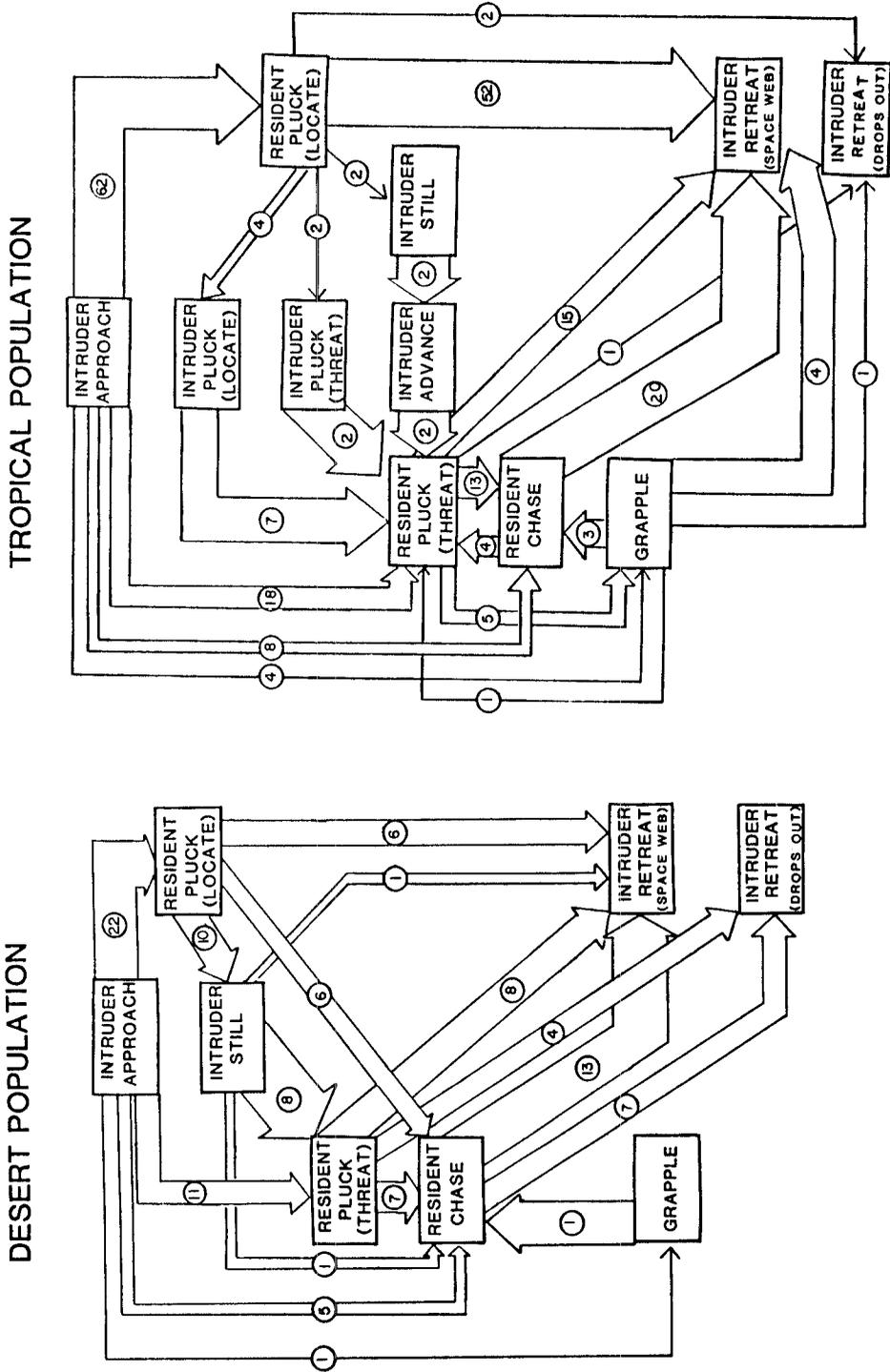


Fig. 5.—Transition frequency diagrams for agonistic interactions between individual *M. spinipes*. Width of arrow is proportional to frequency of transitions from one behavior to another. Number in circle is the actual number of observations: (a) desert population (SMA); (b) tropical population (FDLF).

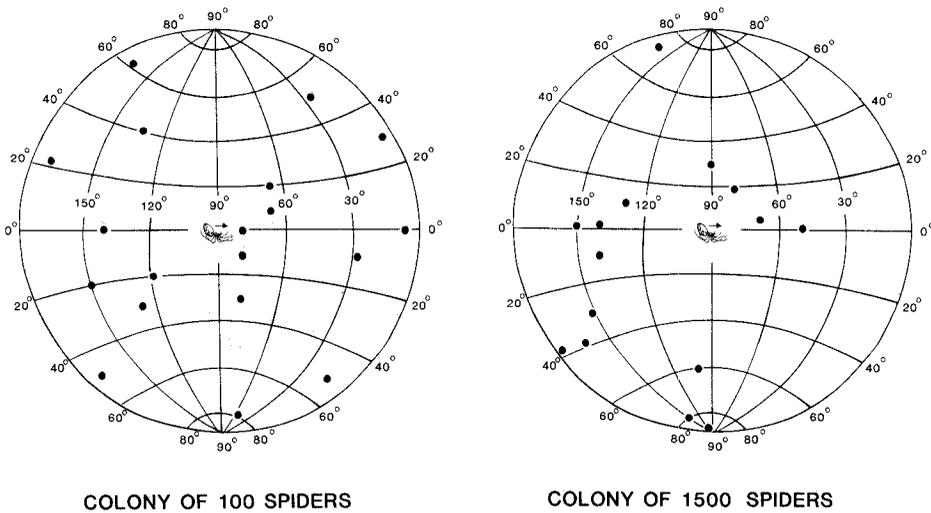


Fig. 6.—Hemispheric projection of *M. spinipes* nearest neighbor locations in Fortin de los Flores (see text for explanation): (a) a colony of 100 spiders; (b) a colony of 1500-2000 spiders.

samples, and conclusions drawn are tentative. Attempts to mate individuals from different populations have yielded inconclusive results. When pairs of males and females were isolated no courtship or mating behavior was ever observed. Egg sacs were produced, but the spiderlings never hatched, and no cause of the hatching failure was apparent. We couldn't determine if this failure to crossbreed is indicative of species isolation, or the result of age incompatibility, or some other factor.

CONCLUSION

Evidence presented here strongly suggests that both environmental and genetic factors influence the variation in spatial organization observed in *Metepeira spinipes* colonies. These findings must then mean that populations from the desert and tropical forest habitat represent either separate genetic subgroups within the species, or newly evolved species with different types of social behaviors. The differences in social spacing and agonistic behavior seen in these populations are likely to be adaptive, and result in improved survival and reproduction in the environments in which they occur. These populations (or species) might then represent early stages in the evolution of increasing social tolerance in spiders.

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