

**MECHANISMS OF THE FORMATION OF TERRITORIAL
AGGREGATIONS OF THE BURROWING WOLF SPIDER
GEOLYCOSA XERA ARCHBOLDI MCCRONE
(ARANEAE, LYCOSIDAE)**

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ABSTRACT. It has long been proposed that aggregations of *Geolycosa* wolf spiders form by limited dispersal from the maternal burrow. In this study I test for conspecific attraction and limited dispersal to account for the formation and maintenance of aggregations of *Geolycosa xera archboldi* McCrone, endemic to the scrub habitats of Highlands County in central Florida, USA. I found no evidence for conspecific attraction in either field tests or observations of natural relocation. I did confirm that hatchlings disperse a short distance from the maternal burrow. The distance hatchlings disperse is influenced by territorial interactions with siblings. Older spiders which were experimentally released also exhibited limited dispersal.

Aggregation by territorial species presents a theoretical problem in that territoriality is by definition partitioning of space away from conspecifics. The hypothesized functions of territorial aggregation fall into two general categories: 1) 'dear enemies', where neighbors are beneficial and; 2) 'conspecifics-as-cues', where dispersing individuals use established conspecifics as cues to habitat quality.

Getty's (1981) competitive collusion model proposed that neighbors might ultimately serve to maximize territory size. This 'dear enemies' model suggests that individuals which settle next to neighbors will be less likely to lose territorial space to later immigrants to the patch. These later immigrants might insert their territories into the unclaimed space between randomly spaced territories and usurp peripheral space from these surrounding territories.

Conspecific attraction occurs when dispersing or relocating individuals use the presence of established conspecifics as site-selection criteria when they choose a site to establish a territory. The use of conspecifics as evidence of habitat quality was proposed as early as 1961 by Orians to explain the phenomenon of territorial aggregation by nesting red-winged blackbirds (*Agelaius phoeniceus*). Stamps (1987, 1988, 1991) has proposed this as the function of conspecific at-

traction by anole lizards (*Anolis aeneus*) on the Caribbean island of Grenada.

I have documented both territoriality and aggregation in *Geolycosa xera archboldi* McCrone, a burrowing wolf spider (Marshall 1994). Clumped dispersion of *Geolycosa* burrows has been noted previously (*G. rafaellana*, Conley 1984; *G. turricola*, Miller 1989; *G. missouriensis*, Richardson 1990). It has been proposed that aggregations of *Geolycosa* wolf spiders form by the settlement of juveniles near the maternal burrow (Miller 1989). However, this has never been quantified nor have alternative hypotheses been tested.

In this study I examine the mechanisms of aggregation formation in *Geolycosa xera*. *Geolycosa xera* is restricted to the scrub habitats of central Florida where it builds burrows in areas of exposed sand (Marshall 1994). These spiders are entirely dependant on their burrows for protection from predators and climatic extremes. All foraging activity is centered on the burrow mouth and *G. xera* does not leave the immediate vicinity of its burrow unless dispersing.

METHODS

The present study was conducted at Archbold Biological Station in Highlands County, Florida. Archbold is a private research facility approximately 10 km S of Lake Placid.

Experimental tests for conspecific attraction.—I tested for conspecific attraction in the summers of 1990 and 1991. I have previously

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observed and quantified dispersal by these spiders in summer (Marshall in press). I used two approaches in my test for conspecific attraction: enclosure tests and field trials. In both these tests I examined the influence of established territory holders on burrow sites chosen by experimentally released individuals I will call 'settlers'. For the enclosure tests I built five 1.0 × 2.0 m aluminum flashing enclosures in an area of suitable microhabitat. The founding population was induced to dig burrows into the end of each enclosure I selected by covering the sand in the other end with leaf litter. I then removed the leaf litter and released one marked settler into each enclosure each night for a week at randomly selected points (using an X, Y coordinate system and a random number table). The morning after release I noted where the settlers had dug their burrows. Settlers which dug burrows in the half of the enclosure with the founders were scored as having exhibited conspecific attraction, and those settlers which had dug burrows in the other end as not exhibiting conspecific attraction.

For the field trials I created four rectangular, open sand patches 1.5 × 3.0 m in oak scrub by raking leaf litter and cutting vegetation to the ground surface, exposing the sand. Studies I have conducted on the ecology of *G. xera* indicate that barren sand is the sole requirement for burrow placement. Two of these were to be test patches with founders, and two were to be control patches without any founding population. Ten founders were established in one end of the founder patches in a two by five array. This founding group was established by setting out 5 cm diameter approximately 20 cm tall clear acetate cylinders spaced 30 cm apart and placing a spider into each cylinder at dusk. It was hoped at this time that they would dig a burrow. Individuals which did not dig a burrow by morning were removed and replaced with another spider the following evening. These cylinders were removed after the spiders built burrows. I used older spiders (burrow diameter > 5.0 mm) as founders, and younger spiders (burrow diameter < 3.0 mm) as settlers (this followed the finding that younger individuals relocate more often; Marshall in press). The distinct size difference between founders and immigrants made it unnecessary to mark the spiders. Over six successive evenings I introduced two settlers 1.0 m apart in the center of each sand patch (for a total of 12 per patch). The next morning I recorded the burrow sites (i. e., which end) they chose and

removed them. To test for non-random dispersal I scored site choice by which half of the patch the settlers dug burrows in. If the settlers were exhibiting conspecific attraction they should preferentially choose the ends of the patches with founders. In the patches with no founding population settlement should be random. To test for non-random settlement I used a Fisher's exact test on frequency of burrow site choice scored by which end of the patch immigrants selected for each pair of patches for each treatment. In the founder patches this was either the half with founders or the half without founders. In the control patches this was either the eastern end or the western end.

Census studies of immigration and recruitment.—In order to test for the influence of local population density on rates of immigration (spiders moving into the area) and recruitment (spiders hatching within the area), I collected census data on naturally-occurring local populations of *G. xera*. I set up 10 pairs of 1.0 m² quadrats in 10 independent patches of sand in the scrub. A patch was considered independent if it had a well-defined leaf litter edge. I selected each census quadrat pair to represent the highest and the lowest spider densities found within each patch. I censused these patches on a weekly basis from 2 April–10 July 1993. At each census new burrows were flagged and measured. Based on observations of natal dispersal, I knew that all spiders with a burrow diameter of 2.0 mm or less were spiderlings and assigned them to the 'recruit' category (in the sense of recruitment into the population by birth). All new spiders with larger burrows were considered to be settlers. Also, previous research (Marshall in press) has shown that these spiders will periodically close their burrows and that 90% of these closure periods will last 14 days or less. For this reason I will consider only the census data from 16 April–10 July in my analysis in order to minimize the counting of residents as settlers when they reopen their burrows during the early part of the census period. At each census any previously flagged burrows were checked, and it was noted whether they were open or closed. These data allow for an estimation of rates of immigration versus recruitment.

Dispersal strategies.—Aggregations of *Geolycosa* wolf spiders have been proposed to form by the settlement of hatchlings in the vicinity of the maternal burrow (Conley 1984; Miller 1989). I tested this by recording the dispersal distances

of hatchlings from five separate sibling groups. I began by observing the burrows of females I knew to be incubating eggs in late June 1991. When I first observed spiderlings in the maternal burrow, I began to check the vicinity of the maternal burrow daily for the appearance of spiderling burrows. I measured the distances of each spiderling burrow from the maternal burrow, its nearest-neighbor distance and its nearest-neighbor's burrow mouth diameter (burrow mouth diameter is closely correlated with body size in *Geolycosa*; McQueen 1983; Miller & Miller 1984; Marshall in press). As the maternal burrows were spaced widely apart, I feel confident that all observed spiderlings were attributed to the appropriate maternal burrow. In order to look for pattern in the data, I used regression analysis of the distance dispersed as a function of days since the onset of dispersal. I predicted that a significant, positive relationship between day and distance dispersed would be evidence of territorial aggregation by the spiderlings. Individuals which dispersed first would establish territories close to the maternal burrow. Siblings that dispersed later would be forced to walk further before digging a burrow by competition for space with previously settled siblings. Only the data from the first 10 days were used in order to limit the recounting of relocating spiderlings. Counting spiderlings twice would violate the assumption of independence of the regression model.

The high rate of relocation found in the 1991 summer field season (up to 3.2% of the population relocates per day; Marshall in press) coupled with the persistence of aggregations raised the question of how individual dispersal strategies might influence patterns of dispersion. In June of 1994 I marked and released 80 individuals in order to quantify individual dispersal distance. The test subjects were juveniles arbitrarily collected from outside the study population. I marked the spiders with a fluorescent powder (Radiant Color, Magruder Color Co., Elizabeth, New Jersey) of a type which has been widely used for both invertebrates and vertebrates (Lemen & Freeman 1985; Fellers & Drost 1989; Morse 1993). I marked the spiders by placing them in a vial containing a small amount of the powder and gently shaking them so as to completely coat the spider. Spiders were held until release in a clean vial. One advantage the use of this powder has over paint marking is that the spiders incorporate the powder coating their bodies into their new burrows. These colored burrow mouths

are very conspicuous in the white sand of the scrub. The spiders were released at sites in suitable habitat at least 30 cm from larger conspecifics. I did this to reduce the chance of cannibalism due to my choice of release site. I released the spiders in early evening (approximately 1800 h) which is the time of day I had most commonly observed relocating individuals. Spiders were released by placing the vial containing the spider open on its side in the sand and then leaving the area. I found burrow sites the next morning by searching the entire sand patch.

I also marked, released, and watched 14 additional individuals until they dug burrows. These individuals were marked with enamel paint on the carapace and released as detailed above. Instead of leaving the area I stepped back to observe from at least 4 m away.

RESULTS

Experimental tests for conspecific attraction.—In the enclosure test there was no evidence for conspecific attraction. The mean proportion of settlers in the five enclosures choosing the end of the enclosures with founders was close to one-half (0.44).

There was no evidence for conspecific attraction in the field trials either. In both the patches with founders and without, settlers settled randomly (Fisher's exact test: patches without founders, $P = 0.54$; patches with founders, $P = 0.19$).

Census studies of immigration and recruitment.—The mean densities for the weekly censuses of the paired plots were significantly different for high versus low density local populations (paired $t = 5.84$, $df = 9$, $P < 0.001$). However, there was no significant difference for immigration rate (paired $t = 1.08$, $df = 9$, $P >$

Table 1.—Summary of regression analyses of natal dispersal of 5 groups of *Geolycosa xera archboldi* at Archbold Biological Station. For the analyses the distance from the maternal burrow that spiderlings built burrows was regressed on the number of days since the initiation of dispersal by the brood that the spiderling burrow appeared.

	<i>N</i>	Sig.	<i>r</i> ²
First group	24	$P = 0.01$	0.26
Second group	19	$P = 0.001$	0.63
Third group	51	$P = 0.006$	0.14
Fourth group	20	$P = 0.0043$	0.37
Fifth group	22	$P = 0.0006$	0.45

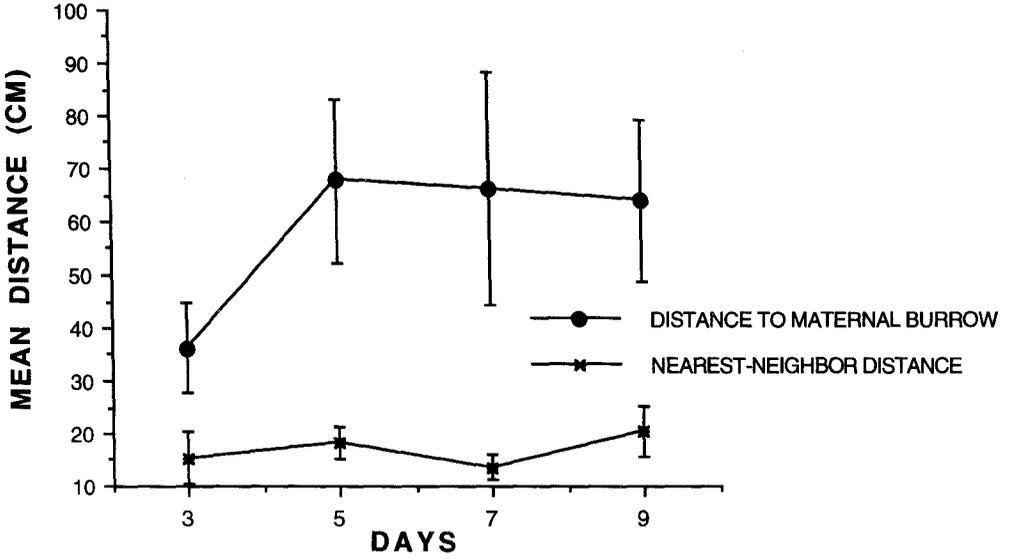


Figure 1.—Cumulative mean dispersal distances (\pm SE) for five cohorts of hatchling *Geolycosa xera archboldi* at Archbold Biological Station, June-July 1991. The two lines represent the mean of values recorded for each spiderling burrow, the standard errors are for an $n = 5$ (for the five cohorts).

0.2) or recruitment rate (paired $t = 0.04$, $df = 9$, $P > 0.5$).

Dispersal strategies.—In all five groups of hatchlings, there was a significant positive correlation between the days since the initiation of

dispersal and the distance dispersed (Table 1). The low R^2 values may be attributed to the spread of distances dispersed on the later dates. While the nearest-neighbor distance remained relatively constant, the distance from the maternal bur-

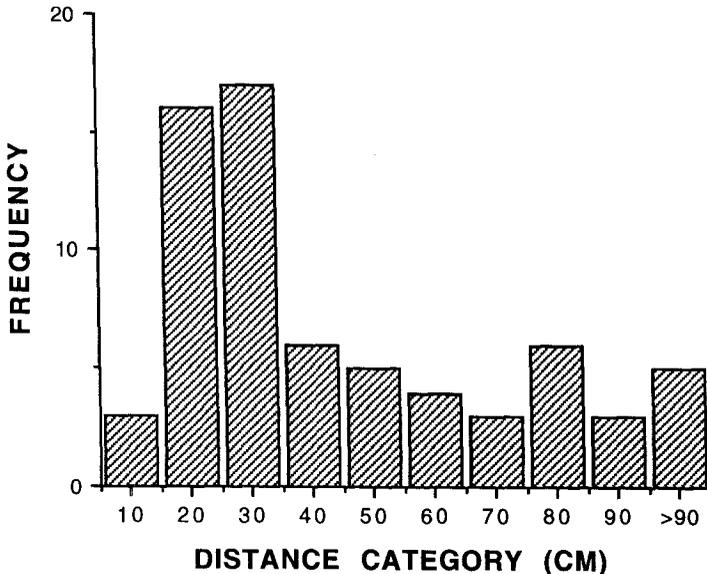


Figure 2.—Frequency distribution of dispersal distances for 68 marked juvenile *Geolycosa xera archboldi* at Archbold Biological Station, June 1994. Distances are from release site to new burrow site.

row increased sharply between days 3 and 6 (Fig. 1). Almost all of these nearest-neighbors were siblings.

I found 68 of the 80 spiders I released. The marked spiders dispersed an average of 43.9 cm before building a burrow (Fig. 2, 43.9 ± 38.4 cm, $n = 68$, range 7–240 cm). My failure to find 12 of the released animals will bias my results to the shorter distance categories as these individuals are likely to have dispersed further than most (an artifact of my own searching behavior).

Out of the 14 experimentally released spiders, 10 settled while under observation. The time to initiate burrow construction was $48:32 \pm 15:23$ min:sec (mean \pm 1 SD). The remaining four took longer than 90 min, and I found them in new burrows the next morning.

DISCUSSION

Territorial aggregations of *G. xera* initially form and are maintained by limited dispersal. Spiderlings leaving the maternal burrow apparently disperse only as far as they have to avoid their territorial siblings. I found no evidence for conspecific attraction in this spider. However, aggregations persist in spite of relocation rates as high as 3.2% a day (Marshall in press). The reason for this seems to be the limited dispersal that these spiders exhibit even when relocating. *Geolycosa xera* is highly mobile on the sand (being an ambush predator), yet over half these spiders settled within 30 cm of the release site. I believe that this limited dispersal is an evolved strategy rather than a maladaptive lack of vagility. Dispersal is assumed to be riskier than non-dispersal (Southwood 1962; Gaines & McClenaghan 1980; Johnson & Gaines 1990). In the case of *G. xera*, an important potential cost of dispersal is the risk of mortality due to cannibalism. *Geolycosa xera* periodically close their burrows (e. g., when molting or after catching a large prey item). These periods of burrow closure last up to two weeks or longer (Marshall in press). Apparently dispersing individuals are unable to assess the location of the closed burrow of a larger conspecific, and I have seen smaller spiders settling within the territory of larger individuals with closed burrows. The correlation of the abandonment of the burrow of the luckless settler with the re-opening of the larger resident's burrow is suggestive. This uncertainty associated with site choice underlies the risk of relocation, making it analogous to dispersing in a mine field. I found no evidence for any ecological predictors of bur-

row site location within the microhabitat (Marshall 1994). Thus, given open sand, I hypothesize that burrow sites are chosen only to avoid active larger conspecifics. There is no advantage to long-distance dispersal, given the uncertainty of the location of closed burrows and the risk implicit in crossing space defended by potentially cannibalistic territory holders.

While inbreeding has been hypothesized as a cost of limited dispersal (Johnson & Gaines 1990), it is not likely an issue for *G. xera*. When male *G. xera* mature, they abandon their burrow and wander in search of mating opportunities. I have observed wandering adult male *G. xera* to move between patches, which I have not observed natal dispersers to do. Presumably, the greater distances travelled by the males in search of matings reduce the probability of inbreeding within these patches of microhabitat.

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