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DISPERSAL AND SURVIVORSHIP IN A POPULATION OF *GEOLYCOSA TURRICOLA* (ARANEAE, LYCOSIDAE)

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Abstract. A population of the burrowing wolf spider *Geolycosa turricola* in Mississippi was monitored over a period of 4 years. Weekly censuses of the number of burrows that were active, open but not active, or inactive were taken. The timing of the dispersal of spiderlings was examined by use of caging experiments. A habitat manipulation experiment was used to assess burrow site preferences. This population reproduced on a 2-year cycle; no young were produced in even years. The results suggest that some dispersing spiderlings construct burrows immediately after leaving their mother's burrow while others overwinter and build their first burrow during the spring. Two dispersing groups are identified and are shown to have different survivorship properties. The importance of this dispersal strategy in terms of subsocial behavior is discussed.

A number of field studies of the population dynamics of the obligate burrowing wolf spiders (*Geolycosa*) have been undertaken in recent years (e.g., McQueen 1978, 1983; Conley 1985). For the most part these studies have confirmed the incidental observations of Wallace (1942): multiyear life cycles predominate (McQueen 1978), dispersal of young from the maternal burrow occurs in the early summer (McQueen 1978, 1983; Conley 1985) and may be by ballooning (Miller 1984a; McQueen 1978), and mortality of spiderlings is high (Humphreys 1976; McQueen 1978). However, several questions regarding the population dynamics of these spiders remain unanswered. Chief among these are questions relating to the timing of initial burrow construction in relation to the onset of dispersal, burrow site preference and tenacity, and the extent to which the timing of dispersal and the size of the dispersing spider affects survivorship. Here we address these issues in a multiyear study of the dynamics of a population of *Geolycosa turricola* (Treat).

METHODS

We studied a population of *Geolycosa turricola* near Starkville, Mississippi, continuously between 1982 and 1985. The population inhabited a 1 ha Selma Chalk deposit (Harper 1857; Miller 1984b) surrounded on three sides by thick growths of southern red cedar (*Juniperus silicicola*) and on the other side by a dirt road. The predominant vegetation, beard grass (*Andropogon* sp.), occurred in large clumps interspersed with bare and litter-covered ground.

A number of small isolated populations of *G. turricola* occurred in similar habitats within a 6 km radius of the study population. These populations were monitored periodically to determine the extent of interpopulation variation in the timing of reproduction and dispersal.

In the fall of 1982 and early spring of 1983, prior to the onset of the dispersal of young, all burrows in the field were marked with numbered surveyor's flags. Beginning in the spring of 1983 the population was censused at approximately weekly intervals between March and October of each year and once a month at other times of the year. During each census, a search of the field was conducted and previously undiscovered burrows of spiderlings were marked. We assumed in this study that changes in burrow diameter represented growth by the spider occupying that burrow. Therefore, the largest diameter (mm) of each newly discovered and previously marked burrow was recorded. Burrow diameter has been shown to be a good indicator of both spider age (McQueen 1978) and size (McQueen 1978; Miller & Miller 1984) for *Geolycosa* spiders.

The state of each burrow was recorded as: (1)

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active (burrow and burrow turret in good repair and/or spider seen in burrow), (2) open/inactive (burrow and turret in disrepair but burrow opening present), (3) disappeared (not found; previously marked burrows only). Burrowing wolf spiders may block the entrance of their burrows with silk and debris during certain times of the year, particularly during late summer through spring (Miller & Miller unpublished data). Because of this, every burrow that was scored as disappeared was reexamined in subsequent censuses. Renewed activity at a burrow previously marked as disappeared resulted in the reassignment of that burrow as active.

We assumed that burrows that appeared active were, in fact, occupied by a spider even though this was not confirmed in every case. Errors in this regard will lead to an overestimation of population size. However, our intent was to study dispersal timing and survivorship not to make estimates of population size or density *per se*. We also assumed that burrows were occupied by the original inhabitant. Studies of the activity patterns of *Geolycosa* (e.g., McQueen & Culik 1981) suggest that this is a reasonable assumption.

A preliminary examination of the census data suggested that dispersal involved two groups of spiderlings of different size (an early summer group of small size and a late summer group of a larger size.) To substantiate this, the size of these two groups was compared. The survivorship of these two groups was compared over two winters (1983 and 1984).

Caging experiments were used to determine whether the beginning of dispersal corresponded to the beginning of burrow building activity in *G. turricola*. In these studies, a wire cage with a 10 cm radius (fine mesh window screen) was placed over six burrows that contained predispersal young. The inside walls of the cages were examined several times each week and spiderlings that were found on the cage wall or on the ground outside the burrow were scored as dispersers and removed. Small crickets were introduced into the burrow periodically (about once each week) for food.

To determine whether newly dispersed spiderlings showed any initial burrow site preference we conducted a habitat manipulation experiment in 1985. Prior to dispersal we altered the habitat within 3 m of eight burrows that contained young. Each circular area was divided into four pie-shaped areas of equal size, and one of the following treatments was assigned to each pie-shaped area: (1) control (no change), (2) litter enhanced (addition of sufficient litter to make a uniform, 2-cm cover in the area, (3) denuded (all grass and litter removed, (4) litter removed (litter raked out, grass left). Because of the small number of burrows used for this experiment, we were not able to completely randomize the experiment. We examined these experimental plots during the normal census and recorded the number and size of the burrows constructed in each plot subsection.

Statistical comparisons of average burrow diameters between months were made with dependent (paired) *t*-tests (t_d) using burrows that were active in both of the months being compared. Independent *t*-tests (*t*) were used to compare distinct sets of burrows (e.g., newly discovered burrows vs previously known burrows).

RESULTS

Comparisons of the reproductive timing of nearby populations with that of the study population revealed that the study population had an unusual breeding schedule characterized by alternating years of production of young. Thus, although some females matured each year in other populations, mature females were found only in alternating years (odd years beginning in 1983) in the study population.

The tabulation of the census data for the generation of spiderlings hatched in the spring of 1983 is given in Table 1. The number of newly discovered and previously marked active burrows is given for each month. The total monthly change in the number of burrows represents the number of active burrows from the previous month plus the number of newly discovered active burrows, minus the number of burrows that disappeared since the previous month (Table 1).

Burrow construction by spiderlings began in July and new burrows were discovered throughout the summer (Table 1). In 1983 a total of 343 burrows were marked between July and October. Most (81.0%) were discovered in July and August (Table 1). In that year, an average of 92.4% of the burrows marked in one month were active in the next month (92.7% July to August, 84.6% August to September, 100% September to October).

There was an increase in the average burrow diameter between July and August 1983. The average diameter of the 141 burrows that were established in July and recorded as active in Au-

Table 1.—Survival history of a cohort of *Geolycosa turricola*. Entries are the number of active burrows (see text). Table includes only spiderlings that hatched in spring 1983.

	Active burrows			
Date	New	Pr. marked	Total	Diameter (SD)
7-83	152	0	152	4.2 (1.03)
8-83	126	141	267	7.0 (1.78)
9-83	60	226	286	6.9 (1.62)
10-83	5	286	291	—
Winter				
3-84	0	139	139	8.2 (2.21)
4-84	136	139	275	8.3 (1.97)
5-84	2	207	209	9.8 (1.61)
6-84	0	149	149	12.3 (2.09)
7-84	0	139	139	14.7 (2.61)
8-84	—	—	—	—
9-84	0	5	5	20.0 (3.74)
10-84	0	5	5	19.3 (3.04)
Winter				
3-85	0	50	50	—
4-85	0	5	5	—

Table 2.—Percentage of overwinter survivors of and burrow diameters of two groups of *G. turricola* spiderlings. July 1983 group includes spiderlings that established burrows during July 1983, August 1983 group includes spiderlings that established burrows between August and October 1983 (see text).

Group	Initial burrow size	% over-winter
First winter, 1983		
July 1983 group ($N = 44$)	4.2 (1.03)	31.6
August 1983 group ($N = 95$)	7.1 (1.78)	68.4
Second winter, 1984		
July 1983 group ($N = 5$)	4.1 (0.98)	23.8
August 1983 group ($N = 16$)	7.4 (1.64)	76.2

gust increased from $\bar{X} = 4.2$ mm (SD = 1.03) to $\bar{X} = 6.9$ mm (SD = 1.79) ($t_d = 11.5$, $df = 140$, $P < 0.001$). The average diameter of the burrows that were established in August ($\bar{X} = 7.1$ mm, SD = 2.11) was significantly larger than the average diameter of the July burrows ($t = 14.53$, $df = 265$, $P < 0.001$). There was not a difference in the diameter of the burrows established in September when compared to the new burrows of August ($t = 1.33$, $df = 178$, $P < 0.001$). Because of the difference in initial burrow size between the July and August spiders, the survivorship of those two groups was examined separately.

Approximately 48% of the burrows that were established in the summer and fall of 1983 (291; Table 1) were recorded as active in early 1984 (139; Table 1). Of these, 31.6% were of the group that initially established their burrows in July of 1983 and 68.4% were of the group of burrows discovered in August of 1983 (Table 2). Fifteen percent of those burrows that were active in 1984 were still active in 1985. Approximately two-thirds (76.2%) of these were from the original August 1983 group (Table 2).

Forty-seven percent of the burrows that were active in October 1983 reopened in March 1984. The average diameter of these spring 1984 burrows was significantly greater than the average for September of the previous year ($t_d = 5.51$, $df = 139$, $P < 0.01$; we obtained no burrow diameter estimates for October of 1983). All of these overwinter survivors remained active into April at which time 136 new burrows were discovered. The average burrow diameter of these new burrows ($\bar{X} = 7.9$ mm, SD = 2.93) was not significantly different than that of the 139 overwinter survivors ($\bar{X} = 8.7$ mm, $t = 0.80$, $df = 273$, $P > 0.05$). The percentage of spiderlings that survived through the spring and summer of 1984 was high ($\bar{X} = 85.1\%$; 100.0% March to April, 75.3% April to May, 71.9% May to June, 93.3% June to July). In the late summer of that year a large percentage of the burrows disappeared. A substantial number of these burrows reappeared as active burrows in the spring of 1985 (35.9%; Table 1). During 1984 the average burrow diameter increased from 8.2 mm to around 20 mm (Table 1). Of the 50 burrows that survived through the winter of 1984–1985, only five of those were recorded active during August of that year. One of those burrows is known to have contained an adult spider with young during the spring of 1985.

The average number of spiderlings taken from cage walls ($N = 6$ cages) during each month of the 1983 caging experiment were: $\bar{X} = 7.5$, SD = 16.3, July; $\bar{X} = 7.6$, SD = 23.4, August; $\bar{X} = 3.0$, SD =12.0, September; $\bar{X} = 0.8$, SD = 0.9, October. Thus, 80% of the spiderlings found on cage walls were found there during July and August. Unaltered (control) plots contained a higher percentage of new burrows than any of the 3 treatment plots (control 40.5%, open 16.2%, litter removed 10.8%, litter added 32.4%.) Burrow disappearance was higher in the treatment areas (control 12.0%, open 26.3%, litter removed 14.0%, litter added 18.0%).

DISCUSSION

Although *G. turricola* was originally thought to have a one-year life cycle (Wallace 1942), our observations (Miller & Miller 1987) indicated that the species has a two-year cycle with a single reproductive period during the second year. This is similar to that reported for other *Geolycosa* (e.g., *G. fatifera* (Hentz), *G. missouriensis* Chamberlin, and *G. pikei* (Marx); Wallace 1942). Mature males appear only in late August and September prior to the final molt of the female. These males may cohabitat with the immature female for a short time prior to her last molt (Miller & Miller 1986) at which time courtship and copulation occur. Once mated, females cover the entrance to their burrow, overwinter there and produce egg cases in the spring (Miller & Miller 1986). Males die after mating in the fall. The young reach reproductive age during the fall of their second year. In our study population, the spiders that survived the winter of 1983–1984 were, thus, of the same cohort rather than progeny of early and late breeding adults of the same year. As we discuss below, the differences in the diameter of initial burrows and the timing of the establishment of these burrows are probably the result of variation in behavior related to the departure from the maternal burrow or the process of burrow establishment itself.

Although the importance of the burrow during all of the life stages of *Geolycosa* is widely accepted, there is still considerable uncertainty about the timing of initial burrow establishment, the factors that affect the positioning of the burrow and the extent to which spiders change burrow locations during their lifetime. With respect to the establishment of the first burrow, the question remains as to whether spiderlings build burrows immediately following dispersal or whether there is a delay between dispersal and burrow establishment during which time spiderlings use natural retreats. McQueen (1978) intimates that construction of first burrows in *G. domifex* Hancock coincided with dispersal although little data for this conclusion is given. Conley (1985) has suggested that spiderlings of the western species *G. rafaelana* (Chamberlin) overwinter in natural retreats and build their first burrows in the spring. However, our observations of several hundred marked burrows of that species in Utah showed that new burrows are constructed in the early fall (Miller & Miller unpublished data). The results presented here for *G. turricola* suggest that both situations may exist in a single population of this species. The onset of burrow construction coincides with the time at which the most spiderlings were found on the walls of cages providing evidence that some spiderlings construct burrows immediately following dispersal from their mother's burrow. However, the census data show that this pattern may not hold for all dispersing spiderlings. A large number (136) of new burrows appeared in the early spring of 1984. It is likely that these are spiderlings that hatched in 1983, overwintered either in their mother's burrow or in a retreat, and then constructed their first burrow in the spring (the strategy suggested by Conley 1985). This is supported by the observation that no young were hatched in the study population in spring 1984, and the average diameter of the spring 1984 burrows was nearly the same as that of previously marked burrows that survived the winter of 1983 (Table 1). Moreover, the Selma Chalk soil inhabited by this population is usually dry and replete with small cracks during the dispersal period. These soil cracks could provide temporary retreats for dispersing spiderlings (Miller 1984a).

A number of researchers have shown that burrow density is not an important factor influencing the survival of *Geolycosa* spiders (e.g., McQueen 1983; Conley 1985). However, the importance of the position of the burrow with respect to physical features of the habitat and, thus, possibly to critical resources, may be important. McQueen (1983) observed that the burrows of *G. domifex* were usually placed in unshaded open areas. One of us (Miller 1984a) addressed the issue of habitat preference in a series of laboratory studies with *G. micanopy* Wallace and *G. turricola*. In those studies it was shown that the tendency to establish a burrow was related to the presence of vegetation and the feeding experience of the spiderling. The study also showed that these factors differed between species. The results of the present study, though limited, corroborate Miller's (1984a) study by indicating that in *G. turricola* burrow sites in grassy areas and grassy areas with considerable litter are favored over open, uncovered positions. The mortality of the spiderlings that established burrows in vegetated areas was somewhat reduced although the study is too limited for a strong conclusion in that regard.

There is considerable uncertainty about whether *Geolycosa* spiders change burrow locations during their lifetime. It is generally thought that such changes are uncommon (e.g., Wallace 1942; Conley 1985). Our observations of over 500 marked burrows in Mississippi (*G. turricola*; this study) and southern Utah (*G. rafaelana*) tend to support this (Miller & Miller unpublished data). The month-to-month decrease in the number of previously active burrows is much smaller than the number of newly discovered burrows. Thus, it is unlikely that those burrows marked as newly discovered are actually spiders that have moved burrow location. Nevertheless, it is possible (perhaps likely) that some threshold of site tenacity exists for most habitats. Indeed, McQueen (1978) suggested that many individuals of the species *G. domifex* change burrow locations during the early spring. The results of the present study do not conclusively rule out burrow position changes in this species, but they do suggest that such activity is uncommon in the population that we studied.

The early survival of burrowing wolf spiders is thought to be extremely low (Humphreys 1976; McQueen 1978, 1983). Humphreys (1976) observed that over three-quarters of the spiderlings of *G. godeffroyi* (L. Koch) in the two smallest size classes died. McQueen found that nearly all (90%) of the young of the year of a population of *G. domifex* in Canada died within several months of hatching. Estimates of adult survivorship suggest that fewer than 10% survive to reproductive age (usually two to three years) (McQueen 1983). The results presented here corroborate the observation of low survival to reproductive age but suggest that high spiderling mortality may not be the rule among the species in this genus.

First winter survivorship in our population was considerably higher than that of populations of other species of *Geolycosa* (e.g., McQueen 1983). Nearly all of the first-year burrows marked as active in 1983 remained active the following spring. Further, the survivorship through the summer of 1984 appears to be high. The decrease in the number of active burrows in the fall of that year is primarily the result of (1) the mortality of adult males that have left their burrows to mate (and subsequently to die; see below), and (2) burrow covering by mated females.

The reason for the high spiderling survival in this population over the first winter is uncertain. The factors influencing mortality of dispersing *Geolycosa* spiderlings are unknown but are likely to include predation, failure to find a suitable burrow site, or parasitism. Mortality factors related to the density of burrows are probably not important (McQueen 1983; Conley 1985). A possible explanation is related to their dispersal strategy. A portion of the broods of *G. turricola* remain in the maternal burrow well beyond the time when successful dispersal is possible whereas other brood members disperse shortly after hatching (Miller 1989). Humphreys (1983) reported the existence of a phasic dispersal pattern in the European tarantula *Lycosa tarantula* (L.). He suggested that such a mixed dispersal strategy might be an advantage in temporally varying environments. Miller (1989) hypothesized that spiderlings in these subsocial groups have a higher chance of surviving the first winter because they build deeper burrows than spiderlings that disperse shortly after emergence from the egg case. The relationship between burrow depth and survival was first recognized by Humphreys (1973, 1978). Although the results presented here do not establish a direct link between subsociality and the timing of burrow construction, they lend support to that hypothesis. Spiderlings constructing burrows in August made larger burrows and enjoyed a higher overwinter survival rate than those constructing burrows in July.

It should be noted that if the spiderlings discovered in August are participants in a subsocial group, the timing of their dispersal is earlier than that predicted from Miller's (1989) laboratory studies. This suggests that the extent to which extended tolerance among *Geolycosa* brood mates exists may be mediated by environmental conditions. Clearly, studies of the spatial, temporal and taxonomic variation in subsocial organization in this genus are needed to delimit the nature and strength of these environmental constraints.

In terms of the total number of active burrows observed during the study, the survivorship over the second winter appears low. Of the 1983 group only 50 survived the winter of 1984–1985 and were recorded active in the spring of 1985, and only five of those (1.7% of 1983 active burrows) were observed to be active beyond March of that year. However, when viewed in terms of the species' life cycle, second winter survivorship is high. If it is assumed that there is no sex-related mortality then approximately one-half of the 139 spiders that were active in July of 1984 were males. As discussed above, these males would mature, mate and die prior to the winter of 1984–1985. The remaining spiders that survive would become mature females and remain in their burrows during the winter of 1984–1985 to produce young the following spring. Thus, the fifty survivors of the winter of 1984–1985 represent a majority of the spiders that would have had a chance to survive that winter.

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