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ECOLOGY OF THE WOLF SPIDER, *LYCOSA*
CAROLINENSIS WALCKENAER (ARANEAE, LYCOSIDAE)
IN A DESERT COMMUNITY

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ABSTRACT

Various aspects of the ecology of *Lycosa carolinensis* Walckenaer have been investigated in a Lower Sonoran Desert community, including surface activities, seasonal activities, and burrow construction. The average home range is 1.1 m² and parts of the home range boundaries are proposed to be limited by changes in topographical relief.

Adults and immatures are inactive from November through February. Immatures reach their highest percentage during the months of March and October. The peak percentage of females and males occur in June and July, respectively. Females have two peaks of egg sac carrying in late July and late August and can possibly have two broods of spiderlings per year. It is thought that females do not reproduce until the third summer and possibly live one year or more. Males also mature in the third summer, but die the year they reproduce.

The burrows occupied by *L. carolinensis* serve as a retreat from heat, desiccation, and some predators. The burrows are randomly distributed with respect to each other but uniformly distributed with respect to shrubs. Most of the burrows have turrets (87%), which probably function as an "early warning system." In the laboratory, 72% of third, fourth, and fifth instar spiderlings construct burrows which they later abandon, giving rise to the possibility that the spider can possess at least two burrows during a lifetime.

INTRODUCTION

In desert regions of North America, only three general studies of spiders have been made (Fautin 1946, Chew 1961, Gertsch and Riechert 1976). Fautin treated spider ecology of communities in the northern desert shrub biome which is dominated by sagebrush, *Artemisia*. Gertsch and Reichert studied the spatial and temporal partitioning of desert spiders in the Chihuahuan Desert of south-central New Mexico. Their study area is characterized by a lava bed, mixed grassland, and rangeland. Chew dealt with the spider ecology in hot southwestern deserts, much like the present study, in an area dominated by creosote bush, *Larrea*. Chew's study only included spiders of the shrub strata because he felt that spiders of the ground stratum were quantitatively much less important.

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Stomach samples taken from lizards showed a low food utilization of ground dwelling spiders, however, Chew pointed out that ground dwelling spiders are probably principally active at night, and may not be adequately sampled by lizards.

From field evidence, I consider that nocturnal ground dwelling spiders, both in size and numbers, play a much more important role in the ecology of a desert community than has been thought.

Lycosa carolinensis Walckenaer is found throughout the United States (Kaston 1953), where in the hot Sonoran desert of Arizona it is active only at night. Specimens collected near Phoenix, Arizona, were identified by Dr. Willis Gertsch of Portal, Arizona, to be *L. c. texana* Montgomery which in Gertsch's opinion possibly is a separate species. Because of its size (up to 12 mm thorax width) and numbers, it could play an important role in the ecology of a creosote bush (*Larrea*), bur sage (*Franseria*) community. Since Chamberlin (1908) revised the family Lycosidae, *L. carolinensis* has been mentioned only briefly by Kaston (1936, 1948), Cole (1946), Kuenzler (1958), Whitcomb and Eason (1964, 1956), Moeur and Eriksen (1972), and Farley and Shear (1973).

Before an assessment of the importance of *L. carolinensis* in the desert community can be made, it is necessary to gather information on certain aspects of the life history, ecology, and behavior of the animal. It was the purpose of this study to investigate the surface activities, seasonal activities, and burrow construction of *L. carolinensis* in the Lower Sonoran Desert.

MATERIALS AND METHODS

Study Areas—In March 1970, a study area (approximately 150 m square) was selected on the Ahwatukee Ranch, Maricopa County, 4 km southwest of Guadalupe, Arizona (elevation 424 m). This portion of the Lower Sonoran Desert is characterized by flat open ground which is occasionally interrupted by shallow washes formed by infrequent run-off.

The flora of the Ahwatukee Ranch study area was analyzed using the point-center quarter method (Cottam and Curtis 1956). The dominant plant is creosote bush, *Larrea tridentata* (DeCandolle) Corville with a relative density of 98% and an actual density of 0.09 plants/m². The remaining 2% of the relative density is made up primarily of scattered bur sage, *Franseria deltoidea* Torrey. Adjacent to the study area, paloverde, *Cercidium microphyllum* (Torrey) Rose and Johnston, and saguaro cactus, *Carnegiea gigantea* (Englemann) Britton and Rose, are present in low densities. Other plant species, including desert annuals and other species of cacti also are present but at lower densities and more scattered in distribution. The soil is sandy and well packed on open expanses, grading to coarse gravel in the bottoms of washes. Under creosote bushes the soil is softer and of finer texture. Extensive surface scratching, burrowing, and digging activities of rodents, lizards, and arthropods, particularly under creosote bushes, are evident throughout the area.

In the late winter of 1972, a second study area, known as the Usery Pass study area, was selected at the junction of Bush Highway and the Usery Pass Road, approximately 52 km northeast of Phoenix, Maricopa County, Arizona. The vegetation of this study area is of the paloverde-bur sage-saguaro type (Lowe 1964). White bur sage, *Franseria dumosa* Gray, is the most abundant dominant. Creosote bush constitutes a minor element in the shrub flora. Scattered paloverde trees and several species of cacti, including saguaro,

occupy the areas between washes. Blue paloverde, *Cercidium floridum* Benthams, and ironwood, *Olneya tesota* Gray, are distributed along the washes along with a relatively lush and varied flora of shrub species.

Surface Activity—Prior to June 1970, several visits were made to the Ahwatukee Ranch for the purpose of locating active spider burrows. The study area was searched after dark several times using a head lamp to create a narrow beam of light that would be reflected from the eyes of the spider. In this manner a spider could be located and by walking over to the spider its burrow also could be found. A small number of spiders were marked with phosphorescent paint as an aid in identification of individuals. Once a burrow was located it was numbered and marked with a wooden stake placed on the north side of the burrow 35 cm from the burrow entrance. During the course of the summer of 1970, any additional burrows that were found on the weekly visits were also marked.

From June until November 1970, weekly visits were made to the Ahwatukee study area. On each of these nightly visits, data were collected at approximately hourly intervals by walking to each active burrow, if the study area was visited from dusk until midnight, or approximately two hour intervals if the visit was from midnight until dawn. At each burrow the position of the spider relative to the burrow entrance was recorded. Data also were collected on any reproductive behavior that was observed or the presence of egg sacs. The distribution of plants and the topography of the ground was mapped for selected burrows to determine more about home ranges.

At the end of the summer, weekly data were compiled and plotted on graph paper to represent the distribution of a spider around its burrow. The outermost points of this distribution were connected by a straight line to form a polygon with the least area. The area of the polygon represented the minimal home range of a particular spider. Using a planimeter, the home range was calculated to the nearest tenth of a square meter.

Seasonal Activity—From March until October 1972, bimonthly visits were made to the Usery Pass study area to collect spiders for the determination of seasonal activity.

On each nightly visit, a random course was walked and approximately 20 spiders were collected at random and preserved in 70% ethyl alcohol. These collected spiders were then brought into the laboratory where sex and carapace width were determined, the latter to be used in ageing the specimens. Dondale (1961) found carapace width to be one of the most reliable morphometric criteria for age determinations.

As each spider was collected, data also were collected on the width of the burrow entrance, height and composition of the turret, presence of tumulus piles, and the distance and species of plant nearest to the burrow.

Field captured spiders of different age groups were brought into the laboratory and introduced into circular metal containers (approximately 18 x 15 cm) two-thirds full of desert soil. These spiders were fed and watered as needed and the soil in their containers was moistened bimonthly. They also were checked weekly for burrowing activity.

RESULTS AND DISCUSSION

Surface Activity—Extreme daily maximum desert soil surface temperatures during the summer, up to 65° C in June (Hadley 1970) and higher in July and August, cause many

desert arthropods to seek subterranean shelter from the heat during the day and to become active at night when temperatures are lower and relative humidity is higher. This species constructs a cylindrical, tube-like, subterranean burrow of approximate body width where it seeks refuge during the day and centers its activity around this burrow at night.

In the Sonoran Desert, this species is almost entirely nocturnal, and during two years of field observation I noted no diurnal movement. However, after heavy summer rains it occasionally has been seen wandering on the surface, probably due to the flooding of the burrow (Honetschlager, personal communication).

The average home range for spiders at the Ahwatukee Ranch study area during the summer of 1970 was found to be 0.8 m² for males (n=9) and 1.2 m² for females (n=15). These differences were not significant using a *t*-test at the 5% level because of the great individual variation. When male and female home range measurements were combined the average home range was 1.1 m² (approximately 9 ft.²).

Only one study to date has measured the home range of lycosid spiders (Kuenzler 1958). By constructing a polygon formed by field location points of the spider at various times, Kuenzler determined the home range of the species in Table 1.

The difference between Kuenzler's results and my results could be due to either habitat differences or sample size differences (3 spiders vs. 23 spiders).

Table 1.—Home ranges of selected species of wolf spiders (from Kuenzler 1958)

Species	Sex	No. Spiders	Average Home Range	
			ft ²	m ²
<i>Lycosa timugua</i> Wallace	Immat.	27	33	3.1
	Male	2	449	41.8
	Female	8	103	9.6
<i>L. carolinensis</i>	Immat.	3	6	0.6
<i>L. rabida</i> Walckenaer	Immat.	2	130	12.1

The shape of the home range was compared to topography and plant distribution, and no clear correlation was found. However, in many cases it appeared that a boundary of the home range was formed by a rapid change in topographical relief. This was particularly noticeable when the home range came in contact with a wash or the mound surrounding a clump of creosote bushes. This delimitation of the home range boundary by rapid changes in topographical relief only occurred when elevational changes were found within a distance of approximately 0.3 to 2.5 m from the burrow depending upon the size and shape of the home range for that particular spider. Figure 1 shows the shape of the home range for female 18 and how her home range is possibly delimited by both changes in topographical relief and the presence of vegetation. I found no discernible delimiting factors for the western edge of the home range. Perhaps there is an innate maximum distance a spider will wander away from its burrow.

The distance from the spider burrow to the nearest shrub was measured to the nearest 0.5 m. When this distribution of distances was compared to a Poisson distribution, it was found that the spider burrows did not occur in a random pattern from the shrubs ($p < 0.01$) but were more uniformly distributed.

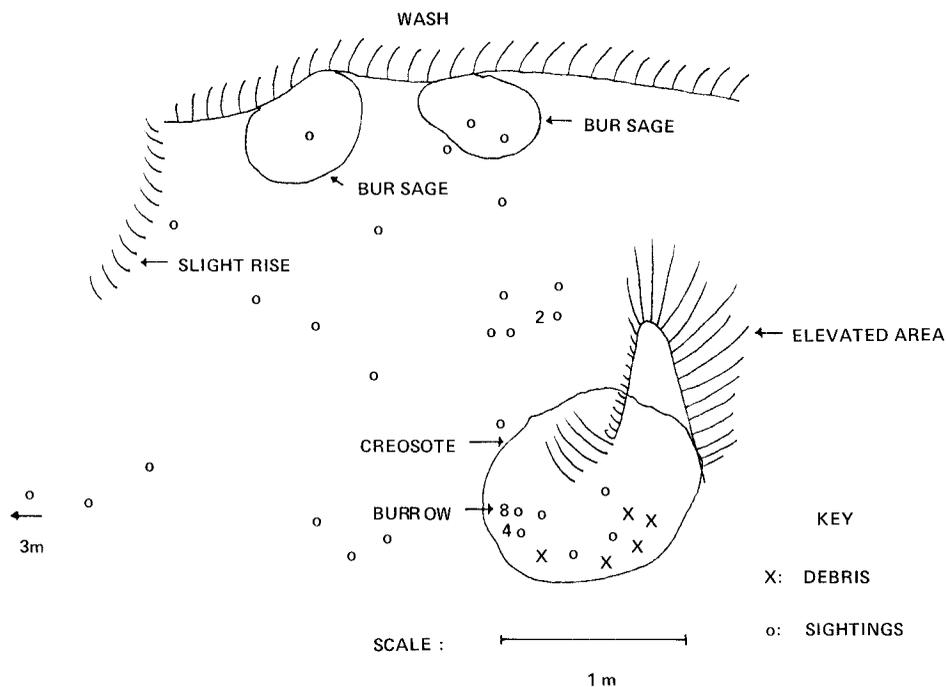


Fig. 1.—Delimitation of the home range of female 18 by changes in topographical relief at the Ahwatukee Ranch study area during the summer of 1970.

Another statistical test (Holgate 1965) was used to determine the distribution of spider burrows at the Ahwatukee Ranch study area. Briefly, random points were chosen and the distance to the two nearest spider burrows was measured. The sum of the ratio of these squared distances was then divided by sample size to obtain an index of distribution, A . According to this test: $A=0.5$, random distribution; $A<0.5$, uniform distribution; $A>0.5$, aggregate distribution. The calculations from the data gathered at the Ahwatukee Ranch produced a value of $A=0.4328$. Although this value is less than 0.5 it is not significantly different from a random distribution at the 0.05 level.

These two tests would indicate that wolf spider burrows were distributed in a random manner throughout the study areas, but at a uniform distance from the shrubs. Both Cole (1946), in a woodland, and Kuenzler (1958), in an old-field habitat, indicate a random distribution for this species.

This random distribution is only valid up to a certain point, because of the cannibalistic tendencies of spiders, no two active burrows were found that had overlapping home ranges. Therefore, interspider distance of burrows was always greater than the maximum wandering distance of the inhabitants of the adjoining burrows and usually, because of the low density of spiders, much greater.

Another explanation of spacing in a desert spider is provided by Riechert (1974). She suggests that the regularity of distribution of webs of the funnel web spider, *Agelenopsis aperta* (Gertsch), in a Chihuahuan desert grassland and recent lava bed habitats in south-central New Mexico is attributed to a social mechanism. The mean spacing of individuals is believed to function to ensure a food base of available prey.

Wolf spiders feeding on the surface were found in very low numbers at both study areas. Out of 674 field encounters with wolf spiders only three were found to be feeding (0.4%). This agrees with Edgar (1969) who found the same infrequent feeding of *L. lugubris* (Walckenaer). Neither this species or *L. lugubris* actively run down their prey but wait until the prey comes close to the spider where it is suddenly captured. This low number could be biased if the spiders left their food upon being disturbed; however, from observations in the laboratory, once a spider captured a prey it was very reluctant to relinquish it. This would indicate that spiders fed infrequently or were capturing prey and transporting it to their burrow to feed

On 7 July 1970, a desert hairy scorpion (*Hadrurus arizonensis* Ewing) was found feeding upon a leg of a female wolf spider about 9 cm from her burrow. She was on the surface and had lost, presumably to the scorpion, all but one leg on the left side of her body. The spider was seen weekly on the surface for the next two weeks before the burrow became inactive.

Other potential predators upon wolf spiders observed in the area include coyotes (*Canis latrans* Say), screech owls (*Otus asio* [Linnaeus]), elf owls (*Micrathene whitney* [Cooper]), and various predatory insects. Cazier (personal communication) has observed the predatory wasp *Cerceris frontata* Say dislodge a wolf spider (*Lycosa coloradensis* Banks) from her burrow.

Seasonal Activity—The monthly percentages of each life stage (immature, adult female, adult male) found at Usery Pass during 1972 are shown in Figure 2. The cross-hatch component of the immature column represents penultimate males. As can be seen from the graph, the highest percentages of immature spiders were found in March and October 1972, the lowest numbers occurred in midsummer. Mature female spiders were found from April through September with a peak number in July, while males also were found in these months, but their peak number occurred in June. No wolf spiders were found active in the months of November through February, and it is known that in cool climates or seasons, wolf spiders enter a state of torpor (Moulder *et al.* 1970). Changes in these populations of “hibernating” spiders are influenced by temperature more than any other physical factor (Elliot 1930).

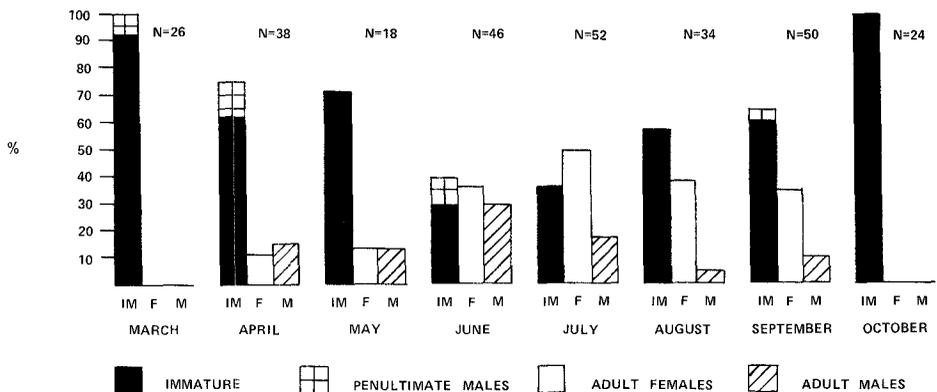


Fig. 2.—Relative percentage of each life stage (immature, adult female, adult male) found in the field during the corresponding month of 1972.

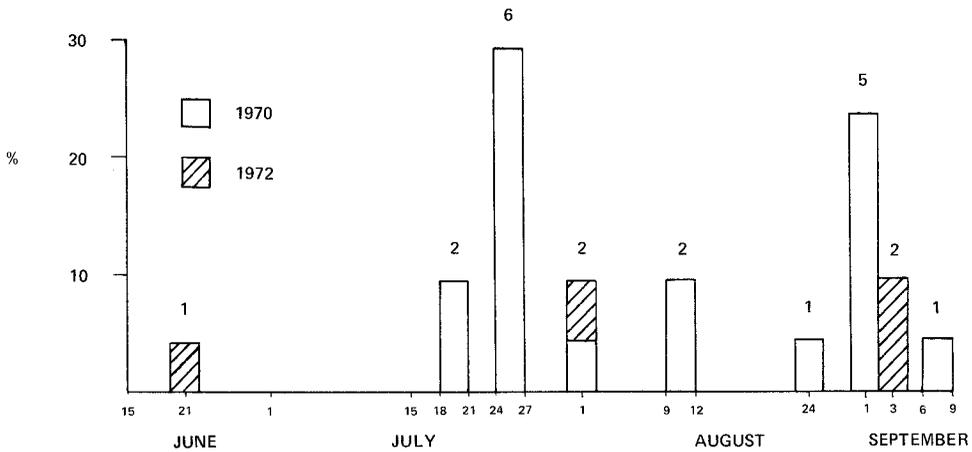


Fig. 3.—Relative percentage of females with egg sacs in the field during different months of the year.

The age classes of spiders above ground during the year was almost opposite to that found by Duffey (1962) in a limestone grassland. He reported that the proportion of adults was never more than 48% during the year, highest in the winter and lowest in the summer (less than 7% in July). The adults in this study were at their highest percentage in the summer, up to 65% in June and July, and at their lowest percentage in the fall. This difference could be for several reasons; first, the adults could “hibernate” at warmer temperatures than the immatures thereby eliminating them from being collected. Second, the immatures might be harder to find at night due to their small size and, therefore, were not collected in the same proportion to their true numbers.

Males were found in their maximum numbers one month before females (June and July, respectively), although in June the percentage of females in the population was higher than that of males as it was for every month (except for April and May). Perhaps males are not as numerous as females in the population or the survival rate of males is less than that of females.

Females were found carrying egg sacs from mid-June to early September (Figure 3), with young on their backs from early July to late September, and that year's young were found in the field from the middle of July to early November.

Figure 3 shows more specifically the period of time that females were found with egg sacs. There are predominantly two main peaks of egg sac carrying, one occurring in the latter half of July and early August and the second occurring in late August and early September. Of 13 egg carrying female spiders observed at the Ahwatukee Ranch during 1970, one was seen on 25 July carrying an egg sac, that young later emerged from, and she was seen carrying a second egg sac on 17, 24, and 31 August. On 8 September, the burrow and turret were in a state of disrepair indicating the spider was no longer active. No young were observed from this second egg sac although in the week between 31 August and 8 September the young could have dispersed. This phenomenon of multiple broods per season has been demonstrated in other lycosids (Turnbull 1966, Vlijm and Kessler-Geschiere 1967).

Female wolf spiders were seen frequently sitting at the top of their burrows, heads down, with egg sacs attached to the posterior part of the abdomen. This behavior was observed primarily before midnight. According to Gertsch (1949) in the diurnal burrowing Lycosidae the female "suns" her eggs during the warmer part of the day to hasten the development. In the desert, the soil surface cools rapidly after sundown (Hadley 1970), air and soil temperatures becoming approximately equal at 2000 hours, while subsoil temperatures lag behind those of the surface. Hadley (1970) found at -20 cm the maximum subsoil temperature in June of 42° C was not reached until 2000 hours. The average depth of 21 burrows that were excavated is 25.5 cm with a range of 18-40 cm. Moeur and Eriksen (1972) found that this species maintained normal activity above 30° C, but as the temperature increased so did the energy requirements of the spider. Perhaps female wolf spiders are selecting a cooler temperature, but one well within the activity range, in which to "incubate" their eggs. Also, from laboratory experience with wolf spider egg sacs, I found that egg sacs were subject to fungus infection in high humidity environments. Hadley (1970) found a relative humidity range of from 55-70% at depths of 20-25 cm. Perhaps by moving to the top of the burrow the egg sac was not subjected to high humidities.

The average measurement for 10 somewhat spherical egg sacs collected in the field and laboratory were $14.1 \times 11.5 \times 10.2$ mm, the mean weight of which was 0.95 g. The sacs contained 112 to 180 eggs with a mean of 149.

Ten females were observed to carry their egg sacs around for a mean of 12.3 days, whereupon the young emerged and climbed upon the female completely covering her abdomen and parts of the cephalothorax and legs. The young remained on the female approximately five days before they dropped to the ground and became independent spiderlings. A few of the young would stay around the mother's burrow for weeks after they emerged but most soon disappeared to find a suitable burrow or construct their own retreat.

In the laboratory, 26 spiders that were raised from spiderlings estimated to be approximately five days old, took on the average an additional 253 days to mature when kept at a constant temperature of 32° C with food and water at one week intervals. During the midactivity season, especially June through August, spiders in the field could easily be subjected to higher temperatures which would speed up development. This would probably be balanced because most of the remaining part of the year they would be subjected to cooler temperatures that would retard development. If a spider hatched in mid-July, in most years it would only have until mid-September to grow under favorable conditions before temperatures cooled and the spider went into a state of torpor for the winter. The next summer could be spent maturing, then the spider would overwinter either as a penultimate or as a mature spider, emerging from its retreat the following spring ready to reproduce in that year. From Figure 2 it can be seen that penultimate males were present both in March and September. The former are probably overwintering spiders that have to molt only once in order to become mature. The latter are males that have almost matured over the summer and are ready to overwinter and reproduce the next year.

It is thought that males die the summer they reproduce. Figure 2 shows a gradual decrease in males from a peak in June until the end of the activity season. Death the year of maturity is a common occurrence for the males of all species (Gertsch 1949).

Females that reproduced in 1970 at the Ahwatukee Ranch were again seen active in 1971. This indicates that mature females overwinter and can reproduce more than just in

the summer they reached maturity. This is supported by the fact that mature females form a much higher percentage of the total population in the latter part of the activity season (July through September) than do the males (Figure 2).

Therefore, field and laboratory evidence suggests that this species probably does not reproduce until their third summer. Following maturity females may live at least one additional summer or possibly more while males die the year they mature. Other authors also have reported biennial species of wolf spiders: Hackman (1954) for *Trochosa pratensis* (Emerton), and Kurata (1939) and Wallace (1942) for *Geolycosa*. Gertsch (1949) found that all burrowing wolf spiders of the United States are large species living more than one year.

Burrows—The function of wolf spider burrows is thought to be one of retreat from the elements as well as from potential predators. Because of extreme daily summer maximum temperatures in the desert the burrow serves as an ideal refuge from heat and lack of moisture until night comes, temperatures cool, and the relative humidity increases. At this time the burrow serves as a center of activity and retreat from some potential predators. At night, this species often would retreat to the burrow at the slightest disturbance even when approached from more than 50 m, while on other occasions a person could approach close enough to capture the spider. On rare occasions, and for undetermined reasons, under harassment the spider would avoid retreating to the burrow and remain on the surface.

Little information is available on the construction or description of wolf spider burrows (see Dumas and Whitcomb 1964, Gwynne and Watkiss 1975, Hannock 1899, Kaston 1948, Kurata 1939, and McCook 1888).

A wolf spider constructs the burrow by spinning a circular-shaped flooring on the ground. She then digs up this mat and moves it to one side with the sand sticking to it. This procedure is repeated until the burrow is dug to the proper depth. The burrow is as big as the spider but enlargements in the diameter of the burrow are made at various levels to allow the spider to turn around (Gertsch 1949).

This species possesses no unique or modified anatomical parts that are used in digging burrows (Gertsch 1949). Its large size and powerful chelicerae are advantageous for digging; however, I propose (from laboratory and field evidence) that this species often does not need to dig its own burrows but possibly takes possession of burrows dug by other desert dwellers such as rodents, lizards, and other arthropods. Several cases were noted of the young taking possession of their mother's burrow at the end of the activity season after she had died or even during the activity season upon the disappearance of their mother. Spiders collected in the field often have a burrow opening with a diameter of 1.2 cm at the surface, but 5 cm below the surface the diameter is 5 or 6 cm, much too large for the spider but approximately the same size as burrows constructed by small rodents found in the area. It would appear advantageous in terms of energy expenditure for spiders not to dig their own burrow if others were available.

Third to fifth instar spiderlings constructed small burrows in the desert soil present in their laboratory containers. Of 70 spiderlings raised in the laboratory 72% constructed small burrows. These burrows were occupied for approximately one instar and then abandoned, and no attempt by the spiderlings to enlarge these burrows was seen. This raises the possibility that these spiders might construct or possess at least two burrows, one when they are extremely small and another as they grow larger.

Of 10 immature spiders brought into the laboratory and housed in metal containers six eventually, after several weeks, constructed burrows. All the spiders constructing burrows matured into females while all those not constructing burrows matured into males. Due to the small sample size it is difficult to know if only females will construct burrows in the laboratory. On other occasions adult wolf spiders did not construct burrows in the laboratory when provided with what was thought to be the necessary materials and optimum edaphic and climatic conditions. *Lycosa narbonnensis* Walckenaer also lives in a permanent burrow and if taken away from the burrow it showed neither the inclination nor ability to dig another one (Savory 1928). The difficulty in getting these spiders to construct another burrow when brought into the laboratory is probably a case of not providing the spider with the proper stimuli instead of the lack of ability on the spider's part to perform this behavior.

The majority of digging and remodeling takes place early in the activity period (March through June). At this time tumulus piles, small mounds of fresh earth, can be found around many of the burrow entrances of all size spiders, indicating digging activity. Later, towards the end of the activity period (August and September) only burrows constructed by that year's spiderlings have tumulus piles present.

Of 76 wolf spider burrows checked, only 10 burrows (13%) did not have a turret (an extension of the burrow above ground usually composed of sticks or grass). The average height of a turret above the soil surface is 1.2 cm. The turret is usually constructed of material found in the immediate area, which is tied together with silk to form a fairly sturdy structure with a smooth lining continuous with the silk of the burrow. The following materials are used by this species to construct the turret: creosote bush and bur sage leaves, dried grasses, small twigs, cholla thorns, small pebbles, and rabbit pellets. The most common materials are small twigs, grasses, and mud. The function of the turret has been proposed by Gertsch (1949) to be that of a lookout; however, for nocturnal spiders the use of the turret for this purpose is probably reduced. I often noticed that the sticks and grasses used in construction of the turret radiate outward from the burrow entrance for several centimeters, and because these sticks and grasses are attached to the lining of the burrow, the turret might serve as an "early warning system" for the wolf spider when it is in the burrow. Vibrations from small animals that moved across these sticks could be transferred down the burrow to the spider thus extending its sensory range. The turret also possibly can prevent water from running down in the burrow during times of excess run-off immediately following light to medium desert rainfall, act as a retardant against intruders, prevent dirt and sand from blowing into the burrow (Gwynne and Watkiss 1975), serve as a recognition signal for the owner, or serve as a place to sit above the hot substrate.

The shape of the burrow varies from a straight vertical tube to a predominantly vertical tunnel with many bends and turns probably representing the path of least soil resistance as the burrow is being dug. Often the bottom of the burrow is slightly enlarged; also, some burrows have exuviae (the cast skin of the spider) attached to the tunnel wall about 20 cm below the surface. Prey remains were not found in the burrows, suggesting that feeding is done above ground.

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