Comparative Ecology of Two Sibling Species of
Wolf Spiders (Araneae, Lycosidae)

By

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DEDICATION

To the memory of my father; he left with me his philosophy of
life:

"Anything worth doing is worth doing right."

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Abstract of Dissertation Presented to the Graduate Council
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COMPARATIVE ECOLOGY OF TWO SIBLING SPECIES OF
WOLF SPIDERS (ARANEAE, LYCOSIDAE)

By

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A previous investigator found that several sibling (cryptic) species of lycosid spiders occurred in mutually exclusive local habitats in northern Florida. The objective of my study was to identify the factors responsible for the local allopatry of two of the species. The first, Lycosa ammophila, is restricted to the sandhill (longleaf pine-turkey oak) community, while the second, L. lenta, occurs in more mesic communities. L. ammophila may have originated from L. lenta or some common ancestor on Pliocene islands having sandhill communities.

Lycosa ammophila shows an array of adaptations to living in the sandhill community which L. lenta lacks. It compensates for extreme daily temperature fluctuation in the sandhill community by breeding only during the wet summer months and by being semi-active during the drier portions of the year. The evolution of this limited activity pattern has occurred in the absence of a marked increase in the ability to regulate water loss physiologically, and has resulted in a two-year life cycle for the species. Lycosa lenta breeds from December through August and typically has a one-year life cycle.

Adaptations of the species to high temperatures are similar. Both show similar behavioral responses when heated, have critical thermal maxima of ca. 48°C and show marked increases in the rate of water loss at ca. 38°C. The latter change is irreversible and suggests a cuticular wax disruption described for many other arthropods.

The larger average size of mature L. ammophila results in a slightly lower percent weight loss per hour during periods of desiccation than experienced by L. lenta. The larger L. ammophila can utilize larger prey, including L. lenta, and better escape predators; however, its greatest hunting efficiency probably occurs in unvegetated areas where it need not climb to forage. This latter requirement correlates with the observed preference of larger instars for open sandy areas both in the sandhill community and in mesic areas when relocated. Lycosa lenta, however, avoids open sandy areas and areas with dense vegetation and prefers regions with well-shaded leaf litter. In these regions, the microclimate is moderate and large L. ammophila are not encountered.

Both species dig burrows, provide them with silken lids, and occupy them during the day. Mature females enlarge a portion of the burrow into a chamber 5 to 6 cm in diameter and 1 to 5 cm deep. The chamber probably functions as a space for construction and holding of the egg sac and for hatching of the young.

Home ranges for mature females of both species averaged about 2.5 m². Lycosa ammophila females had larger home ranges than L. lenta females in the same habitat.

Reproductive isolation results not only from different habitat preferences but from cues, perhaps chemical in nature, associated

with the dragline silk of females and perhaps the females themselves, which males use in avoiding females of the other species. The courtship behavior of the two species appears to be identical.

INTRODUCTION

Past studies of spider ecology related plant associations and microhabitats with the species of spiders inhabiting them. Elliot (1930) was one of the first to quantitatively show spatial and temporal orderliness of certain species in the beech-maple forest community. Since that time, numerous reports of specific spider-plant associations appeared. Such studies included the following habitat types; shores, dunes and piedmonts (Barnes, 1953; Barnes and Barnes, 1954; Berry, 1968; Duffey, 1968; Lowrie, 1942; Lowrie, 1948), forest areas (Branson and Batch, 1968; Gibson, 1947; Huhta, 1965; Lowrie, 1968; Luczak, 1959; Luczak, 1966; Peck, 1966), prairies, meadows and fields (Bailey and Chada, 1968; Barnes and Barnes, 1955; Breymeyer, 1969; Dondale et al., 1970; Duffey, 1962; Kajak, 1963; Muma and Muma, 1949), deserts (Bixler, 1970; Chow, 1961) and studies of islands (Drew, 1967; Truman, 1942). Many authors suggested that specific niche requirements of each species (temperature, humidity, specific food types, isolation from predators and competitors, et cetera) were most available in the habitat where it was normally found, but few attempted to test their hypotheses.

Several investigators examined the microclimates and physiological requirements and tolerances of individual species more closely (Hackman, 1957; Lagerpetz and Jaynas, 1959; Mørgaard, 1956). Others analyzed ecological niches and relationships of two or more species (Cloudsley-Thompson, 1957; Kuenzler, 1958; Mørgaard, 1951). Van Hook

(1971) analyzed the energetics of a grassland community in which lycosids were the major consumers. These studies provided some of the information necessary to explain the microhabitat preferences and distribution of sympatric, and even congeneric, species.

In one study, Wallace (1938) found that wolf spiders (Lycosidae) in the Gainesville, Florida region were distributed in specific habitats. These data correlated with the discovery that Lycosa "lenta" was a complex of at least eight South-eastern United States species, each having a more-or-less typical local habitat preference (Wallace, 1942). He noted, for example, L. lenta (sensu strictu) occurred in mesic habitats ranging from swamps and low hammocks through the mesic hammock (the local climax community) and palmetto-pine flatwoods. It ranged from central-Florida north to the Appalachian Mountains and west into Texas. The species appeared also in drier plant association, the xeric hammock and old field communities. It rarely existed in the longleaf pine-turkey oak (Pinus palustris-Quercus laevis) community. Instead, one of the sibling species, L. ammophila, found exclusively in north Florida, occurred in this community. L. ammophila also inhabited old field communities and was normally more abundant than L. lenta. On the basis of this allopatric distribution in local habitats and marked differences in male and female genitalia, Wallace described L. ammophila, a new species related to L. lenta.

Wallace emphasized the sharp segregation of the two species at the ecotone between the longleaf pine-turkey oak and neighboring communities, often the xeric hammock community. He noted the correlation between the presence of leaf mold and shade and the presence

of L. lenta and the absence of L. ammophila and suggested that these factors were the major niche parameters not shared by the species.

In the current study, I sought to identify the factors responsible for the allopatric distribution of L. lenta and L. ammophila. I examined the physical characteristics of the mesic habitat and the longleaf pine-turkey oak habitat, the life history of the species, their reproductive biology, their physiological adaptations to xeric conditions, characteristics of the burrow, the home range, and their habitat preferences.

DESCRIPTIONS OF STUDY AREAS

During the two-year study, I used eight field stations, three intensively. Four stations have longleaf pine-turkey oak (sandhill) communities while three have mesic communities. The eighth is a segment of road with turkey oak on one side and pine flatwoods on the other.

Station 1 (29° 29' 9" N, 82° 15' 38" E)

This station, 5.3 km due east of the Alachua County Court House, is the type locality for L. ammophila. Wallace (1938) described it as "an almost pure stand of turkey oak, with practically no undergrowth of any kind." This area now has many young live oaks (Quercus virginiana) and less open sand is present. Annual weeds are encroaching from adjacent areas. A non-wooded area in the center of the station supports an "old field" community of grasses and weeds where both L. lenta and L. ammophila occur. Only L. lenta inhabited neighboring xeric hammocks, judging from extensive field work.

Station 2 (29° 42' 50" N, 82° 27' 29" E)

This station, located 9.8 km north of the intersection of Highway 26 and S-329 on S-232, is a typical turkey oak community. Leaf drifts have developed against wire grass clumps (Aristida stricta and Sporobolus gracilis), resulting in numerous open patches of spottily shaded sand. The turkey oak community grades into a slash pine flatwoods (Pinus australis) and then into an extensive mesic hammock known locally as San Felasco Hammock.

Station 3 (29° 38' 14" N, 82° 23' 32" E)

This station, located 2.1 km west of S. W. 34th Street on S. W. 20th Avenue, in Gainesville, was the L. ammophila habitat studied most intensively. It is primarily a turkey oak-wire grass community. The southern boundary is S. W. 20th Avenue; xeric hammock, composed almost entirely of live oak and laurel oak (Quercus laurifolia), borders on the remaining three sides. The primary portion of the area used for study (Figure 1a) was a rectangle 7,700 m² and included five distinct habitats. There was a xeric hammock (c) on one border, an old field community (b) on another, and turkey oak and wire grass (a) on the remaining two. Dense grass (Panicum spp.), 30 to 60 cm in height (d) dominates approximately one fifth of the area. The remainder of the area, with the exception of some sandy roads (e), is turkey oak and an unusually dense growth of wire grass. Few open sand areas like those in Station 2 were present. Typical herbaceous plants of the community also occurred (Laessle, 1968).

North of the study area ca. 100 m, a power line right-of-way has been cut through the xeric hammock and portions of turkey oak areas. It is ca. 20 m wide, oriented east and west, and supports an atypical old field flora. Prominent components of the right-of-way community are small seedlings of live and laurel oak annually cut down in the spring by maintenance crews.

Station 4 (29° 41' 57" N, 82° 15' 43" E)

This very atypical turkey oak community lies 2.2 km east of State Highway 24 on the Gainesville Municipal Airport Road. It consisted of a cleared strip of land at the end of a run-way ca. 0.3 km wide. Species characteristic of the longleaf pine-turkey oak

Figure 1. a. The study area at Station 3. The habitat types are as follows:

- a. turkey oak with dense wire grass,
- b. old field community of annual weeds and patchy open sand,
- c. live oak hammock (xeric hammock). The ecotone between live oak and turkey oak is bounded by the dashed lines,
- d. tall dense grass, and
- e. sandy roads (cross-hatched).

b. The study area at Station 5 is bounded by roads (cross-hatched) and a small stream (stippled). The two habitats are:

- a. tall grass and annual weeds, and
- b. scattered low grass with extensive areas of leaf litter and mulch.

The roads and the area to the right were not studied.

community had invaded it. Adjacent areas are of planted pine suggesting that the entire region may have supported the sandhill community before man's influence. Few trees were over 4 m in height and herbaceous plants were abundant.

Station 5 (29° 38' 35" N, 82° 20' 39" E)

This L. lenta habitat, intensively studied during the summer of 1970 and early spring of 1971, lies on a hillside immediately to the south-east of Bartram Hall on the University of Florida campus. Vegetation of the 5,400 m² area varies, in part, with soil type (Figure 1b). Very large loblolly pines (Pinus taeda) grow in the pebbly-clay of the top portion of the hillside (habitat a) while live oaks dominate the more sandy lower habitat (b). An understory is absent throughout, but grasses and annual weeds cover most of habitat "a" and reach heights of several meters by late summer. A more undisturbed woods with dense understory and extensive leaf litter occurs farther down the hill to the south-east. The nearest sandhill community is Station 3, about 6 km west.

Station 6 (29° 33' 42" N, 82° 21' 29" E)

The second intensively studied L. lenta habitat was the Medicinal Garden, 0.3 km west of Bartram Hall (Figure 2). It became necessary to move to this area in 1971 as a result of construction near Station 5. The area is generally more mesic in nature than any of the other stations. The 14,600 m² area studied included a small stream and six rather distinct habitats. Habitat "a" has ample shade and dense annual weeds; "b" has similar shade with an extensive pine needle litter; "c" has dense, unshaded, lawn grass; "d" has lightly shaded, lawn grass intermixed with patches of bare sand;

Figure 2. The study area at Station 6 includes several groups of ornamental shrubbery (dashed lines) and a small stream (stippled). The habitats are:

- a. well-shaded with dense annual weeds,
- b. well-shaded with extensive pine needle litter,
- c. unshaded dense lawn grass,
- d. lightly shaded lawn grass intermixed with patches of bare sand,
- e. well-shaded tall dense grass, and
- f. well-shaded with sparse tall grasses and extensive leaf litter and mulch.

"c" has tall, well-shaded, grasses with little leaf litter; and "f" has sparse, tall, well-shaded, grasses and appreciable leaf litter and mulch. The presence of Lake Alice 120 m south and 1 to 1.5 m lower in elevation than the study area contributes to its mesic nature.

Station 7 (29° 25' 8" N, 82° 42' 37" E)

The most typical mesic hammock examined during the study exists 8.0 km north of the intersection of State Highway 26 and S-329 on S-232. It has all of the plant species characteristic of the mesic hammock (Laessle, 1942) and a heavy leaf litter. Limited access to this property restricted its use.

Station 8 (29° 23' 46" N, 82° 42' 12" E)

This very artificial habitat is the roadside grass on the road east of the "Devil's Millhopper." It lies 5.3 km from the intersection of State Highway 26 and S-329 on S-232. The woods on the west side of the road are primarily xeric hammock species while the east side consists of a mixed old field-turkey oak community. Lycosa lenta occurs on the grass bank of the road's west side while L. amnophila predominated in the road's east bank.

METHODS AND MATERIALS

Field Observations

I collected most of the field data for this study between June, 1970, and June, 1971. During this year, visits to Stations 3, 5 and/or 6 were at two-to three-day intervals or less during the spring and summer and at one-to two-week intervals during the fall and winter. Visits to other stations at irregular intervals were for comparing population activities with the primary three under observation. I recorded date, time, air temperature, humidity, day of last rain, and condition of the sky on each collecting trip. Other observations included predators, prey, descriptions of burrows, and other species encountered. Numbers, instar, and sex of spiders seen or collected and notes on their condition and place of capture were made.

I used several methods to characterize the physical environments in the various communities. From September, 1970, through June, 1971, two model 1000 recording thermometers made by Marshalltown Mfg. Inc., Marshalltown, Iowa, recorded weekly temperature fluctuations from sensors placed at various locations and depths in the soil at the three primary study areas. The seven-day paper disc charts, calibrated in $^{\circ}\text{C}$, provided a permanent record for laboratory analysis. Station 3 data are from September, 1970, to April, 1971; Station 5 data are for April, 1971; and Stations 3 and 6 were measured in May and June, 1971.

In addition to the rainfall-humidity data taken on each collecting trip, similar data were available from the University of Florida Agronomy Department in conjunction with E. S. S. A.

Identification of individual spiders in the field involved a marking technique. Ten-dram plastic snap-top vials held recently collected, mature spiders while they were carried to the laboratory. CO₂ from a fire extinguisher anesthetized the spiders and each such spider received a painted number on its cephalothorax before it revived. Marks painted on the cephalothorax could not be scraped or groomed off by the spider, and, at the same time, did not disturb any of the numerous sensory organs on their legs. The paint was Testors Butyrate Dope. Release of marked spiders to the field occurred the following evening or as soon as possible.

During the summer of 1970, I tried to return marked spiders to the exact point of collection. Wood doweling stakes, 10 to 20 mm high and 2 to 3 mm in diameter, and having a strip of Scotchlite[®] reflector tape around the top 2 cm, marked the capture location and each subsequent resighting point. A piece of Time[®] laboratory label tape about 8 cm long was pressed around the dowel below the reflector tape and pressed together to form a "flag" for the recording of data. I mapped Stations 3 and 5 at the end of the summer and determined the positions of all undisturbed marker stakes.

During the winter and spring of 1971, I shifted to a determination of the survival and movements of spiders when displaced to different areas in their community or to different communities. From December, 1970, through March, 1971, I released at Station 3 58 marked L. lenta collected at Station 5. I placed a marking stake at the location of

each resighting. Five open cages made of 0.4 m by 3 m strips of heavy acetate plastic glued into rings were set into the ground at various places; each held a specimen. Unfortunately, vandals destroyed four of these cages.

From December, 1970, through June, 1971, marked L. ammophila from Stations 1, 2, 3, and 8 were released in various habitats in Station 6. At the same time, marked L. lenta collected at Station 6 were released along with L. ammophila. At each resighting I used marking stakes with the date, number, and species of the spider inscribed on the tape flag.

Laboratory Procedures

The maps of each station with the locations of release and resighting points were used to calculate home range areas. Only data from individuals resighted four more times were used; the outermost resighting points of these spiders defined the sides of a polygon. I used a Keuffel and Esser Planimeter to measure the area bounded by the polygon.

Morphological comparison of the two species involved leg length measurements, cephalothorax measurements and weights. I used twenty-seven L. ammophila and 24 L. lenta females in the first two determinations. These samples represent collecting and preserving from all stations. The four legs from the right side of each specimen were removed and mounted, using Duco^(K) cement, to a glass microscope slide, fully extended and in a row. A measuring microscope provided the longest length of each segment of each leg to the nearest mm. The cephalothorax lengths (the distance between the notch over the pedicel and the furrow between the anterior median eyes) were determined using the same instrument.

Adult spiders were weighed during physiological studies in 1969, and 1970. I determined weights, to the nearest tenth of a milligram, of every mature spider prior to marking from January through May, 1971. An estimation of nutritional and reproductive state also was made. Gravid and well-fed females were often indistinguishable. I assumed that well-fed, mature females partition most energy into reproduction and soon become gravid. I therefore classified all females having a greatly distended abdomen as gravid.

At the outset of the study, a check on the validity of the species seemed in order. The possibility that there was a behavioral and genetic compatibility between them or that they were merely variant populations of a single polymorphic species had not been examined. Two types of breeding tests were performed. The first test used mature males and non-gravid females of each species collected from various habitats and at various seasons. Finger bowls, 20 cm wide, each containing ca. 2 cm of moist sand, held the isolated individuals. Some groups were fed during acclimation; others received no food. After 6 to 15 days, each male was placed into a bowl with a female. Each of the four possible pairings was made.

I tested for the presence or absence of species-specific pheromones using the techniques of Hegdekar and Dondale (1969). Filter paper discs were cut to fit the bottom of 8 cm-wide jars. Isolation of mature females of each species in such jars varied for periods of one to seven days. Immediately after removal of the females, observations followed the behavior of single males.

Determinations were made for these five primary physiological characteristics of the two species: (1) water loss characteristics at various temperatures and humidities, (2) temperature of cuticular

wax breakdown, (3) critical thermal maxima (and behavioral responses as the temperature was increased to that point), (4) resting metabolic rate and (5) ability to survive in a saturated atmosphere.

The water loss studies began following an acclimation period of at least seven days with water continuously available. Following an initial weighing, individuals of each species were confined in glass cylinders 5 cm long and 2.2 cm wide with each end covered by a nylon mesh having holes 0.4 cm in width. For spiders small enough to escape through this mesh size, I substituted pieces of ladies' nylon hosiery. The squares of screening material were held in place by rubber bands. The acclimation chamber used in the study is an Environette by Lab-Line Instruments, Inc., adjusted to maintain the desired temperature and relative humidity. The photoperiod was a 12-hour light - 12-hour dark cycle. Air circulated at an average velocity of 3.8 cm/second. Specimens were weighed at 12-hour intervals until consistent weight changes were observed.

I used the same materials and methods to test for a cuticular wax breakdown point and used only penultimates or adults. In addition, I made weighings and temperature changes at two-hour intervals. The experiment began at 35°C with a saturation deficit of ca. 26 mm Hg. I increased the temperature 2°C and adjusted the humidity to the original saturation deficit at the end of each two-hour interval. I terminated the study at 43°C.

For the determination of the critical thermal maximum for each species, I used an apparatus modified from Nørgaard (1951). A 7 cm wide, 20 cm long glass cylinder with a fine mesh copper screen on the bottom held each individual. A thermistor probe extended close to the bottom of the cylinder through a large rubber stopper

sealing the top. A 4-liter jar with a relative humidity of 50% maintained by a saturated MgNO_3 solution served as a chamber for the cylinder. I then submerged the entire apparatus in a 55°C circulating water bath. This outside temperature produced a heating rate of from 2.0 to 0.5°C per minute in the environment of the spider. I recorded data on behavioral changes and associated temperatures. Temperatures producing irreversible paralysis in the spiders are the critical thermal maxima of this study.

J. F. Anderson made the metabolic rate studies. Mature females of each species, acclimated for ca. 14 days in sealed jars with free water and a meal of one adult field cricket per week, were used for determining metabolic rate, to be expressed as $\mu\text{l O}_2$ consumed/g hr. The last feeding occurred at least two days before the determination. Spiders were weighed the day before and confined in a glass vial, 9.5 cm by 2.2 cm, taped to the opening of the respirometer flasks. This technique allowed the spiders a brief period to adapt to the flasks. A Gilson Differential Respirometer measured respiration rates the next morning. Consistent values from at least four ten-minute experimental periods were used to determine an oxygen consumption value for each specimen. These gross values were converted to $\mu\text{l O}_2$ consumed per gram hour.

Individuals were placed in sealed jars with moist sand to determine whether a differential species mortality occurs in very moist environments. Spiders were acclimated at 25°C and fed one adult field cricket each week. I weighed each one to two days following feeding. I determined dates of death and final weights when possible.

RESULTS

The Habitats

Temperature and Rainfall

Soil temperature data for various habitats, microhabitats and depths appear in Tables 1 and 2. The average daily high and low temperatures for the various locations are in Table 1, and the average temperature fluctuation for each locale during the given time interval is in Table 2. Several facts are evident from these data. First, maximum surface temperatures differ from 20° to 35°C, depending on the season, between the open sand surface in the sandhill community and the shaded leaf litter of mesic hammock. This is especially clear in Figure 3. However, by about 19:00, it is cooler on the open sand in Station 3 than on the leaf litter of Stations 5 or 6. Second, the surface under heads of wire grass and, less often, turkey oak leaf litter is no more than a few degrees warmer than the surface in a shaded mesic area. A similar observation is true for the shaded xeric habitat. Third, temperatures are nearly constant at a depth of one to two inches below the surface (just underneath the leaf litter) in the shaded mesic hammock. However, under open sand in the turkey oak community, temperatures fluctuate two to five degrees, depending on the season, at a depth of seven inches. Fourth, at the depths where temperatures are nearly constant in the two communities, the mesic hammock is 3 to 4°C warmer.

Mean daily high and low soil temperatures ($^{\circ}\text{C}$) at Stations 3, 5, and 6.

Station	Habitat	Dates	Surface		2.5 cm		5.0 cm		7.5 cm		17.5 cm	
			Hi	Lo	Hi	Lo	Hi	Lo	Hi	Lo	Hi	Lo
3	unshaded bare sand	17/IX - 1/X/70	54.9	20.3	43.7	21.8	--	--	--	--	--	--
		2/X - 15/X/70	47.0	18.7	--	--	33.8	21.2	--	--	--	--
		16/X - 28/X/70	34.0	17.3	--	--	--	--	24.6	19.7	--	--
		9/II - 22/II/71	30.0	6.0	--	--	--	--	21.1	9.1	--	--
		7/IV - 21/IV/71	48.8	11.6	--	--	--	--	--	--	--	--
		21/IV - 28/IV/71	--	--	30.9	19.3	--	--	--	--	--	--
		30/V - 2/VI/71	64.0	19.0	--	--	--	--	--	--	--	--
		3/VI - 4/VI/71	--	--	50.0	23.0	--	--	--	--	--	--
		5/VI - 6/VI/71	--	--	--	--	38.0	23.0	--	--	--	--
		6/VI - 11/VI/71	--	--	--	--	--	--	32.0	24.0	--	--
3	turkey oak leaf litter	11/VI - 18/VI/71	--	--	--	--	--	--	--	--	31.0	26.0
		2/II - 9/II/71	40.0	6.9	--	--	--	--	--	--	17.0	13.4
		3/III - 11/III/71	26.4	12.9	--	--	--	--	--	--	17.0	14.9
3	under wire grass	23/II - 2/III/71	28.4	13.3	--	--	--	--	--	--	--	--

TABLE 1 Continued

Station	Habitat	Dates	Surface		2.5 cm		5.0 cm		7.5 cm		17.5 cm	
			Hi	Lo	Hi	Lo	Hi	Lo	Hi	Lo	Hi	Lo
3	shade xeric	23/II - 2/III/71	23.3	13.9	--	--	--	--	--	--	--	--
5	shade mesic	7/IV - 21/IV/71	24.0	14.4	19.9	19.7	--	--	--	--	--	--
6	shade mesic	30/IV - 2/VI/71	35.0	20.0	--	--	--	--	--	--	--	--
		3/VI - 11/VI/71	--	--	24.0	23.0	--	--	--	--	--	--

TABLE 2
Mean daily soil temperature fluctuations (°C) at Stations 3, 5, and 6.

Station	Habitat	Dates	Surface	2.5 cm	5.0 cm	7.5 cm	17.5 cm
3	unshaded bare sand	17/IX - 28/X/70, 9/II - 22/II/71, 7/IV - 21/IV/71	26.9 (.9)*	-----	-----	-----	-----
		17/IX - 1/X/70, 21/IV - 28/IV/71	-----	20.4 (.4)*	-----	-----	-----
		2/X - 15/X/70	-----	-----	12.8 (1.3)*	-----	-----
		16/X - 28/X/70, 9/II - 22/II/71	-----	-----	-----	8.0 (.8)*	-----
		30/IV - 2/VI/71	35.0	-----	-----	-----	-----
		3/VI - 4/VI/71	-----	27.0	-----	-----	-----
		5/VI - 6/VI/71	-----	-----	13.0	-----	-----
		6/VI - 11/VI/71	-----	-----	-----	8.0	-----
		11/VI - 18/VI/71	-----	-----	-----	-----	5.0
		2/II - 9/II/71, 3/III - 11/III/71	21.6 (2.9)*	-----	-----	-----	-----
3	under wire grass	23/II - 2/III/71	11.8 (4.2)*	-----	-----	-----	-----
3	shade xeric	23/II - 2/III/71	8.6 (2.6)*	-----	-----	-----	-----

TABLE 2 Continued

Station	Habitat	Dates	Surface	2.5 cm	5.0 cm	7.5 cm	17.5 cm
5	shade mesic	7/IV - 28/IV/71	9.6 (1.0)*	0.1 (.1)*	-----	-----	-----
6	shade mesic	30/V - 2/VI/71	15.0	-----	-----	-----	-----
		3/VI - 11/VI/71	-----	1.0 (0.5)*	-----	-----	-----

*numbers in parentheses are the standard errors of the means for the means given.

Figure 3. Mean surface temperatures during the afternoon and evening at localities in Stations 3 and 5. Temperatures of the open sand at Station 3 were from 22 to 25°C warmer than the shaded areas at Station 5 during the two time intervals studied. However, by about 19:00, surface temperatures were lower at Station 3 than at Station 5.

The mean monthly high and low air temperatures and the mean rainfall for Gainesville, Florida, appear in Figure 4. These regional data have limited predictive value due to the effect of plant communities on the local conditions, the uneven distribution of summer thunderstorms and the annual variability of the weather. The correlation between macroclimate and activity of spiders follows in a later section.

Based on Tower's (1932) study of the evaporation rates in plant associations of north-central Florida, a prediction of moisture as a limiting factor, especially in the sandhill community, is logical. Tower's study, conducted during winter and spring, revealed evaporation rates (determined with dark and light bulb atmometers) were twice as high in the turkey oak community as in the mesic or xeric hammock. During this study, I found, however, the relative humidity at the soil surface in turkey oak almost always over 80% by an hour after sunset with the dewpoint reached most nights, especially during the summer. The moisture evaporating during the day becomes available, therefore, to small animals at night. During periods of extended drought (three to four weeks), free water was less available and spiders became less active.

The soil is always saturated within the first inch below the surface in the mesic hammock. The same condition was true of the turkey oak community except during periods of drought when the first few inches of sand were completely dry. Moisture remained much longer around the roots of wire-grass clumps.

The Fauna

An analysis of the crepuscular and nocturnal fauna of the mesic hammock and sandhill communities is unavailable; however, a number of

Figure 4. Sixty-year mean monthly high and low air temperatures (measured at 1.5 m) and the sixty-year average monthly rainfall for Gainesville, Florida. Data from the Agronomy Department, University of Florida, in conjunction with E. S. S. A.

striking differences became apparent during the study. First, segregation of L. lenta and L. ammophila into their respective habitats was essentially as Wallace (1938) noted. Lycosa ammophila remains absent from mesic community collections and infrequently occurred more than 10 m within a xeric hammock; however, L. lenta males and females appeared rarely in turkey oak and wire-grass collections.

In the power line right-of-way north of Station 3, L. lenta was common at the south shaded borders adjacent to the xeric hammock. Lycosa ammophila was most common in areas bordered by turkey oak. There was a sizeable area, however, where the two species coexisted. Coexistence was also quite evident at Station 8, the roadside bordered by mesic and xeric habitats. Several times, each of the species existed within a meter of each other. Coexistence occurred likewise on the roadside bordering Station 2.

Other wolf spider species characteristically inhabited each habitat. In the mesic areas examined, L. riparia occasionally occurred. The mature females of this species are the same size as L. lenta females and constitute the largest lycosid competitor. Other smaller species present include L. helluo (restricted to wetter areas), L. hentzi (infrequent), L. pulchra (infrequent and reproductive only in winter), and Schizocosa crassipes and S. ocreata (very small and restricted to leaf litter).

In the turkey oak community, L. carolinensis is fairly common. This very large spider can kill both L. lenta and L. ammophila. Lycosa hentzi is abundant but hunts off the ground in wire grass or weeds. Lycosa parthenus is a small species restricted to the leaf litter. Other species present are L. pulchra, L. rabida and L. punctulata, which hunt while climbing.

Vertebrate predators include Bufo terrestris and Scaphiopus holbrooki. These toads were present in both primary habitat types but were in much greater abundance in the turkey oak community, especially following spring rains.

The Species

Comparative Morphology

A comparison of the cephalothorax length and width for adult females of the two species appears in Figure 5. Although the ranges are not exclusive, the means are significantly different (95% confidence intervals shown). The average cephalothorax length of L. armophila is 12% larger than L. lenta while the average width is 10.5% larger.

A comparison of leg lengths in adult females appears in Figure 6. In all cases, the range of the lengths do not overlap the 95% confidence interval for the means. Average lengths of legs 1, 2, 3, and 4 of L. armophila are 22%, 18.5%, 18.3% and 16.5% longer than similar legs of L. lenta.

The average weights of mature females taken from the field are not significantly different during winter and spring (Table 3). In April, a significant difference in mean weights of non-gravid females occurred, while in May, all three categories of mean female weights differed significantly ($P < 0.05$). This difference remained in the laboratory stock where spiders had ample food and during the summer for uncategorized field samples. During the late spring and summer, the average weight of L. armophila in the field is ca. 0.3 to 0.5 g heavier than L. lenta. The lower average weight for L. armophila females during the winter and spring is due to an absence of gravid

Figure 5. Mean cephalothorax length and width for samples of adult females. The rectangles define the 95% confidence intervals; the ranges observed are indicated by the vertical lines.

Figure 6. Mean leg lengths of adult females with 95% confidence intervals (rectangles) and ranges (vertical lines). Ranges of each species are exclusive of the confidence intervals for the other species for all four legs.

TABLE 3

Mean weights of field collected adults, in grams.

Date	All females		Non-gravid		Gravid females	
	<u>lenta</u>	<u>ammophila</u>	<u>lenta</u>	<u>ammophila</u>	<u>lenta</u>	<u>ammophila</u>
January, 1971	0.928 ±0.087	0.907 ±0.223	0.790 ±0.120	0.907 ±0.223	1.009 ±0.086	---
February, 1971	0.884 ±0.060	0.773 ±0.163	0.721 ±0.0607	0.773 ±0.164	0.976 ±0.075	---
March, 1971	1.014 ±0.066	1.091 ±0.668	0.704 ±0.090	1.091 ±0.688	1.071 ±0.088	---
April, 1971	0.834 ±0.055	0.939 ±0.071	0.734 * ±0.042	0.882 ±0.058	0.959 ±0.80	1.134 ±0.127
May, 1971	0.773* ±0.033	1.252 ±0.1164	0.700* ±0.041	1.088 ±0.106	0.993* ±0.074	1.685 ±0.163
May, 1969#	1.000* ±0.096	1.444 ±0.151	---	---	---	---
July, 1970#	0.756* ±0.072	1.093 ±0.095	---	---	---	---
July, 1969	0.754* ±0.094	1.274 ±0.156	---	---	---	---
January, 1971** through May, 1971	0.485* ±0.023	0.792 ±0.026				

*significantly different from comparable l. ammophila data

**males

#fed in laboratory for one to three weeks before weighing

individuals. Twenty to 40 percent of the female L. ammophila collected during these months had collapsed abdomens while only five percent of the L. lenta were in this condition.

Lycosa ammophila males are significantly heavier than L. lenta males. With the exception of three specimens from the cumulative sample size of 147, the weight ranges were exclusive with all L. ammophila weighing 0.6 g or more.

A sample of 15 penultimate L. ammophila taken in January and February, 1971, had a mean weight of $0.8993 \text{ g} \pm 0.0785$ ($P = 0.05$). This average weight is significantly larger than non-gravid L. lenta for all months tested except during January, 1971, but is not significantly different from mature L. ammophila for winter and spring months until May, 1971. This evidence suggests that the moult to maturity may occur during a period of fasting in L. ammophila.

Natural History

Numbers of mature spiders by sex for each species, recorded monthly from April, 1970, through May, 1971, appear in Figure 7. The relative abdominal size served to classify females as gravid or non-gravid during 1971. The major differences between the two species are: (1) the reproductive peak for L. ammophila is one to two months behind L. lenta; (2) L. lenta can and does reproduce during the late winter and the spring; and (3) both species show a marked reduction of apparent adult population size in August. The breeding peaks of L. lenta at Stations 5 and 6 follow exactly the L. lenta population at Station 3.

The absence of gravid L. ammophila during winter and spring and the one- to two-month lag behind L. lenta in breeding peaks accomplishes

Figure 7. Numbers of unmarked mature spiders observed each month. During 1970, search areas were about 8,000 m²; in 1971, they were about 15,000 m². No attempt was made in 1970 to categorize females as gravid or non-gravid. Females with distended abdomens collected in 1971 were classified as gravid.

a similar lag in appearance of females carrying egg sacs in the field, females with second instar young on their abdomens, and the development of immatures through the winter. By January, third and fourth instar L. lenta were absent in the field in contrast to similar instars found for L. ammophila.

Lycosa ammophila was most active in the winter and early spring on all warm nights (20°C). Penultimate L. ammophila were common on such evenings while adults were infrequent. During the same time period, L. lenta was most active on warm humid nights. Adults of L. lenta were generally more abundant than penultimates. On evenings when the temperature was 10°C at sunset, none of the larger instars of either species were active. At temperatures of 8°C or below, all sizes were inactive and remained in their burrows.

In late spring and summer, L. ammophila were most active on evenings when the ground was damp following late afternoon rain storms. Lycosa lenta were most active one to three evenings after the rain shower.

The average life span and time required to reach maturity are not available for either species. One L. ammophila female marked on July 14, 1970, appeared approximately seven months later on February 28, 1971. It had overwintered as an adult and lived at least 200 days; no L. lenta overwintered. The longest field existence of any L. ammophila male is 27 days while a L. lenta male lived 23 days after being marked and released. These values are not maximum possible age limits as the spiders might have migrated out of the study area or simply escaped resighting.

The marked inactivity of L. ~~annophila~~ during much of the winter and the two month lag in development (compared to L. ~~lenta~~) are indirect evidence for a two-year minimum life cycle. Lycosa ~~lenta~~ seems to have a one-year life cycle, but overlapping generations of each instar make analysis confusing.

The influence of predation on population size of the species is unknown. Following marking and release, 50% of the spiders never reappeared and their fate was unknown. Approximately 10% of mature spiders observed at Station 3 had one or more legs missing. This value is higher than exists for Station 5, suggesting heavier predation in Station 3. This leg damage occurred for only 2 to 3% of the L. ~~lenta~~, and equally among the sexes for both species. This difference in leg loss may result from larger populations of vertebrate predators in turkey oak than in mesic areas. Parasitism by hymenopterans was approximately equal in both species at 1 to 2%.

Records of prey being eaten in the field appear in Tables 4, for L. ~~annophila~~, and 5, for L. ~~lenta~~. Observations apply to spiders 1-1/2 cm long or greater. Both species appear to be opportunistic feeders, taking prey species in relation to their availability. Lycosa ~~annophila~~ fed most frequently on large Carpenter ants (Camponotus spp.) common in the turkey oak community. Lycosa ~~lenta~~ caught more beetles than any other type of prey; locally common Pill Millipedes (Glenosis spp.) were the second most frequent prey. Five mature L. ~~lenta~~ and two L. ~~annophila~~ males were found eating in the field.

The degree of cannibalism was small, especially considering the high population densities of smaller instars. It is probable that each individual has a home range providing a degree of exclusive use. This attribute may reduce encounters between individuals.

Field observations of lycosa ammophila prey.

Number of Observations												
Month	Ants; Formicidae;	Camponotus sp.	Noctuid moth	Cricket; Gryllidae	Spiders; Lycosidae;	L. ammophila	Beetles; Scarabidae;	Carabidae;	Cerambycidae	Vertebrates; Toad;	Bufo terrestris	Misc. Diptera
January	1		1			1*						
February												
March												
April	1		1*	1-1*		1*						
May	3					1**						
June						1**		1				1
July			1*			1**		3		1***		
August												
September												
October												
November	1											
December												

* male spider observed feeding

** prey species L. lenta, mature female

*** spider died within 12 hours after feeding

TABLE 5

Field observations on L. lenta prey.

Month	Number of Observations												
	Phalangidae	Spiders; Lycosidae; <i>L. lenta</i>	Noctuid moth	Noctuid moth larva	Beetles; Scarabidae; Cerambycidae	Centipedes; Scolopendridae	Pill millipede; Glomeridae	Slug; Gastropoda	Crickets; Gryllidae	Mayfly; Ephemeroptera	Ant; Formicidae	Roach; Blattidae	Earthworm; Oligochaeta
January	1												
February		1											
March													
April	1	1	1		1								
May					5		2					1	
June		1		1	5		2	1	1	1	1	1	1*
July			1*	1			1						
August													
September													
October													
November													
December					1								

*male spider observed feeding

Two cases of interspecific predation between the two species exist from Station 6 where release of marked individuals of both species occurred. In both cases, mature female L. ammophila killed mature female L. lenta, one of which was carrying young. One of the L. ammophila observed weighed 0.1 g less than the L. lenta; the other weighed 0.6 g more.

Reproductive Biology

Field observations

Mature members of each species exist nearly every month of the year (Figure 7). Copulation by L. lenta in the field was observed January 25, 1971 (J. F. Anderson; personal communication) and June 16, 1971. Wallace (1938) observed copulation in September. Pairs will copulate in the laboratory (25°C) every month. I did not observe copulation by L. ammophila in the field; however, copulation occurred in the laboratory when matings were attempted in February and the summer months.

Females with egg sacs were rarely seen in the field. Three L. lenta records are June 1, 1970, June 16, 1970, and June 26, 1970; however, no L. ammophila sightings were made. In the laboratory, L. lenta females made egg sacs in late February and early March. Lycosa ammophila first made them in late March and early April. The females ate nearly all these egg sacs one to three weeks after construction. Perhaps fertilization never occurred.

Observations of females in the field carrying young were more frequent. Seven L. lenta records exist, the earliest on May 10, 1971, and the latest on July 8, 1970. The earliest of six L. ammophila observed was May 27, 1971, while the latest was July 3, 1970. These

spiders carried no marks and had not been previously observed. In addition, these females were usually moving when sighted and were not resighted on subsequent nights. I also noted that first instars frequently were distributed linearly about 1/2 m on the ground suggesting that they had left their mother as she was moving.

Mating experiments

The courtship sequences of the species as observed in the laboratory were indistinguishable. A mature male placed into a large dish holding a female began, while walking about, exploratory reaching with his forelimbs. As he approached (and occasionally touched) the female, she raised her forelimbs and rushed toward him. Following contact, this brief attack terminated with the spiders facing each other and standing quietly with forelegs raised and touching. Following a period of one to five seconds, their forelegs moving against each other, the female lowered her legs and cephalothorax. The male responded by climbing over her cephalothorax, turning her abdomen with his forelimb and beginning copulation. Alternate palps insert into alternate sides of the epigynum, following abdominal rotation, at six to eight second intervals; copulation was 30 seconds to 8 minutes in duration.

When the females were fasted for one and one half weeks or more, the pattern could be sequentially modified in three ways. First, the intensity of the initial attack increased and lasted several seconds before the female became quiet. In some cases, the male disengaged and left the female; in extreme cases she bit and killed the male during the initial attack or pursued and attacked him again following disengagement. These females were receptive to other males a few nights after feeding. Second, once quiet, the female refused to

lower her legs and appeared to rear back, spreading her fangs. After a few seconds of leg touching, the male reached between her forelimbs with his front legs simultaneously pushing outward. Third, the male reached back to the posterior lateral edges of the cephalothorax and front of the abdomen, stroking these areas with the ends of his forelimbs. If the female did not lower her forelimbs, the male either withdrew his legs and walked away or was attacked.

The response of gravid females to approaching males was similar to that of fasted females; copulation never occurred. Fasted, gravid females responded to males as potential food.

Attempts at mating L. lenta with L. ammophila were unsuccessful. A male of one species placed into a dish with a female of the other, would remain motionless for periods of 20 minutes or more even without first contacting the female. When the male finally did move, the raised forelimb search pattern described above was lacking. He climbed the side of the jar, as if to escape. Females in these attempted crosses either ignored the males, fled from them or pursued and attacked them. The response seemed to be influenced by the size of the male in relation to the female and the length of time since the female had fed. Microscopic examination of the sand in the bottom of the containers revealed an abundance of dragline silk 25 to 50 μ in diameter in several of them.

Males placed on filter paper previously exposed to females, responded as though females were present. When placed in containers where females of their species had resided, males either groomed or immediately began the raised forelimb search behavior. When placed where a female of the other species had lived, the males stood for

3 to 15 minutes without moving before exhibiting escape behavior. Whether the response was elicited by an airborne chemical or by contact with the dragline silk was not determined.

Comparative Physiology

The relationship between the log of body weight and the log of water loss/hour at three different temperature and humidity combinations for various sized spiders of each species is shown in Figure 8. Rates of water loss differ for both species at the low temperature, low humidity and high temperature, high humidity combinations; the elevations of the regression lines are significantly different with individuals of L. ammophila having a lower water loss/hour than an equivalent sized L. lenta. At the low temperature, high humidity combination, that more typical for spiders active at night, the slopes of the regression lines are significantly different with L. ammophila appearing to have an advantage when large and L. lenta when small (below 0.1 g).

In order to compare the species in terms of actual survival time under the environmental conditions described, it was first necessary to determine the relationship between percent weight loss/hour and initial body weight (Figure 9). Smaller spiders lost a higher percentage of body weight/hour than larger ones under the low temperature, low humidity and high temperature, high humidity conditions. In the latter environment, individuals of L. ammophila lost a significantly lower percentage than L. lenta. At low temperature, high humidity conditions, no significant difference in percent weight loss existed for either species or any weight individual. The percent weight loss/hour for a 1.0 g L. lenta and

Figure 8. Relationships between total water loss per hour and initial body weight at three temperature-humidity combinations.

*SIGNIFICANT AT 0.01 LEVEL

Figure 9. Relationships between percent weight loss per hour and initial body weight at three temperature-humidity combinations.

* SIGNIFICANT AT 0.01 LEVEL

a 1.0 g L. ammophila at 25°C, 55% R.H. was 0.144 and 0.120 respectively. At 35°C, 90% R.H., a 1.0 g L. lenta lost 0.138% body weight/hour while a 1.0 g L. ammophila lost only 0.114% per hour.

The mean percent weight loss/hour for individuals of 1.0, 0.1 and 0.01 g of each species multiplied by 24 gives the percent weight loss/day. These values divided into 24, the approximate mean lethal weight loss determined for the species (L. lenta = $24.69\% \pm 1.65$; L. ammophila = $23.11\% \pm 1.22$; $P=0.05$) give estimates of the number of days spiders of each weight could survive at each saturation deficit. These estimations appear in Table 6. In view of the facts that: (1) differences are insignificant between the species percent weight loss at 25°C, 55% R.H., the highest saturation deficit used, (2) no significant difference in % weight loss occurs between any-sized individual of either species at 25°C, 90% R.H., and (3) that the drying effect of the circulating air in the experimental chamber for all saturation deficits is not a factor of the spiders' microhabitat, I assume these humidity and temperature combinations do not function to segregate the species. However, at 35°C, 90% R.H., a situation possibly encountered by spiders in deep burrows in unshaded open sand in the afternoon, L. ammophila would be able to live longer than L. lenta if both species had no access to water.

A number of distinct behavior patterns were noted as the critical thermal maximum approached for both species. Spiders were normally inactive when placed into the cool (20°C to 25°C) test apparatus. As the temperature increased they began to move. The first movement exhibited by the spiders was either slow walking, reaching through the bottom screen with the forelegs or attempted climbing. The

TABLE 6

Estimated survival differences for various weight classes of Lycosa lenta and L. ammophila*.

Temperature and Relative Humidity	Weight (g)	Species	Estimated mean survival in days	Advantage ** in days
25°C	1.0	<u>lenta</u>	7.00	----
55 ± 5%		<u>ammophila</u>	8.30	1.30
sat. def. of 11.26 mg Hg	0.1	<u>lenta</u>	4.20	----
		<u>ammophila</u>	5.00	0.80
	0.01	<u>lenta</u>	2.50	----
		<u>ammophila</u>	2.80	0.30
35°C	1.0	<u>lenta</u>	7.16	----
90 ± 5%		<u>ammophila</u>	9.00	1.84
sat. def. of 4.18 mg Hg	0.1	<u>lenta</u>	4.65	----
		<u>ammophila</u>	5.60	0.95
	0.01	<u>lenta</u>	3.00	----
		<u>ammophila</u>	3.45	0.45

*based on observed mean % weight loss per hour under laboratory conditions described in text. Lethal % weight loss due to dessication assumed to be 24%.

**estimates for 25°C, 55 ± 5% R. H. are calculated from insignificantly different weight loss data.

behavior, "forelegs extended through screen," suggests spiders were either searching for a burrow entrance or were attempting to go deeper in the tube. Not all spiders exhibited this behavior; some immediately began trying to climb out of the tube. This "first climbing," a type of escape behavior, occurred in all spiders. Climbing spiders were very active and often mixed this behavior with "forelegs extended through screen" in rapid sequence. These three behavior patterns would result in thermoregulation if the spiders could escape to a cooler locale.

As the temperature increased further, spiders showed evidence of neurophysiological disturbances. First, they showed a loss of equilibrium. They fell over on their backs while attempting to climb and appeared to have difficulty righting themselves. Those acclimated at 30°C tended to begin walking in a jerky, uncoordinated manner rather than falling over. At temperatures nearing the critical thermal maximum, spiders became inactive for lengthening periods of time. Spiders cooled following this "heat torpor" (Heath et al., 1971) showed no evidence of neurophysiological damage the next day.

At the critical thermal maximum, ca. 80% of the spiders showed an irreversible paralysis. It followed a period of convulsion lasting 4 to 8 seconds. The remaining spiders observed died quietly without convulsions or paralysis.

A summary of the temperatures first producing these behavior patterns appears in Table 7. The temperatures of onset for thermoregulatory responses were quite variable except for 20°C acclimated L. lenta and the differences observed were probably not biologically significant for any-sized spider of either species at either acclimation

Average temperature ($^{\circ}\text{C}$) for responses to heating following acclimation* at 20°C and 30°C

species, acc. temp, numbers, wt. range	forelegs** extended through screen	first movement	first climbing	loss of equilibrium or jerky walking	lack of movement for 15 sec or more	paralysis (critical thermal maximum)
<u>amphibila</u>						
20 ⁰						
N = 13	34.5 $\pm$ 8.74	36.0 $\pm$ 1.99	40.0 $\pm$ 2.11	45.0 $\pm$ 0.54	46.5 $\pm$ 0.33	48.0 $\pm$ 0.25
0.08 - 1.0 grams						
<u>amphibila</u>						
30 ⁰						
N = 15	36.5 $\pm$ 2.26	36.5 $\pm$ 2.22	40.0 $\pm$ 1.39	46.5 $\pm$ 0.20	47.0 $\pm$ 0.27	47.5 $\pm$ 0.26
0.05 - 1.04 grams						
<u>lenta</u>						
20 ⁰						
N = 14	39.5 $\pm$ 0.11	37.0 $\pm$ 0.16	41.0 $\pm$ 0.16	44.5 $\pm$ 0.63	45.0 $\pm$ 0.65	47.5 $\pm$ 0.28
0.002 - 0.83 grams						
<u>lenta</u>						
30 ⁰						
N = 11	36.0 $\pm$ 2.22	35.5 $\pm$ 2.80	38.5 $\pm$ 2.16	46.5 $\pm$ 0.39	46.5 $\pm$ 0.56	47.5 $\pm$ 0.54
0.04 - 0.55 grams						

*for 5 to 14 days

**see text for description of apparatus

temperature. There is a trend for L. lenta to begin each behavioral pattern at a lower temperature when acclimated at 30°C than at 20°C, while L. ammophila does not change.

The onset of neurophysiological disturbance and final collapse occurred with much less variability than the behavioral responses at lower temperatures. Acclimation to 30°C elevated the initial temperature for "loss of equilibrium" and "lack of movement" 0.5 to 1.5°C for both species but did not result in a significant difference between the species. Acclimation did not change the critical thermal maxima for either species.

The investigation of water loss rates at high temperatures (Figure 10) failed to reveal any difference between the species. However, an increasing rate of increase in water loss occurred as the spiders lost the ability to regulate, suggesting cuticular wax disruption (Beament, 1961). Regression lines calculated for the points at 39°, 41° and 43°C both intersect the species lines for lower temperatures at ca. 38° to 38.5°C. After being heated to 43°C, well above the suspected wax transition temperature, these spiders were returned to the 25°C, 55 ± 5% R.H. acclimation conditions and allowed to desiccate for 24 hours. Water loss rates were determined over a 12 hour period. Both species had a percent weight loss/hour approximately twice that of spiders not heated to 43°C (Control = 0.14%/hr; Experimental = 0.26%/hr).

The resting metabolic rates of mature females of both species were essentially identical. Anderson (1970) reports a mean value for 80 L. lenta of $94 \pm 10 \mu\text{l O}_2/\text{g hr.}$ The mean value for 12 L. ammophila examined in this study was $96.6 \pm 12 \mu\text{l O}_2/\text{g hr.}$

Figure 10. Mean percent weight loss per hour at high environmental temperatures with 95% confidence intervals. Saturation deficit was held constant at about 26 mm Hg. The sharp increase in water loss at about 38°C is suggestive of cuticular wax disruption described for numerous insects.

The study of mortality rates of mature females held in jars with wet sand revealed no differences between the species. During the 38-day study, two of nine L. lenta and two of nine L. ammophila died. There was no apparent cause of death in any case; one of the L. ammophila had a light infestation of probably harmelss mites (genus unknown) about the mouth parts.

Burrow Characteristics

I found a total of 32 L. lenta and 9 L. ammophila burrows. Descriptions appear in Tables 8 and 9. Both species typically build a trapdoor at the mouth of their burrow. These trapdoors probably contribute significantly to the retention of water vapor within the burrow. The silk doors and lining of the wall around the mouth of the L. ammophila burrows were thicker than for L. lenta. The former were typically spongy and ca. 1.5 mm thick while the latter were compact and only ca. 0.5 mm thick or less. Often, burrows of L. lenta lacked any noticeable silk reinforcements around the mouth. The trapdoors also served to camouflage the burrow. Sand grains, bits of leaves and other litter in the vicinity were always woven into the top of the doors of both species. Those burrows lacking trapdoors were under dense pine needle or leaf litter or among dense shoots of a clump of grass.

The nature of the burrows varied with the size of spiders, their reproductive state and, perhaps, with the species. In neither species was the burrow silk-lined beyond the mouth to any extent. The burrows of L. lenta can be characterized as follows: (1) the presence of an enlarged chamber at or near the mouth of the burrow is typical only of mature females during the reproductive period. The appearance of

TABLE 8

Burrow characteristics of *Lycosa lenta*

Age* Sex	Chamber			Burrow		Branches		Date
	Door	Depth (cm)	size (cm)	Length (cm)	Angle**	Length (cm)	angle**	
1.2 cm imm.	yes	----	-----	36.0	0°	----	----	6/VI
pp ♀	yes	6.5	4.8 diam	-----	----	----	----	5/I
	yes	----	-----	7.5	90°	----	----	31/I
	yes	----	-----	1.2	20°	----	----	4/II
	no	----	-----	1.2	90°	10.0	50°	26/II
p ♀	yes	----	-----	5.8	90°	----	----	1/III
	yes	----	-----	2.5	80°	15.0	180°	11/III
	no	----	2.5 diam	-----	----	5.0	45°	18/V
	yes	----	-----	10.0	90°	----	----	4/II
p ♂	yes	----	-----	7.5	90°	----	----	4/II
	yes	----	-----	10.0	90°	----	----	26/II
	yes	----	-----	1.2	90°	1.2	180°	26/II

*imm. = immature; pp = prepenultimate;

p = penultimate

**approximate angle measured from the horizontal

Age* Sex	Camber		Burrow		Branches		Date
	Depth (cm)	size (cm)	Length (cm)	Angle**	Length (cm)	angle**	
m ♀							
	yes	1.2	7.5 diam	----	----	----	8/VII
	yes	---	2.5 diam	----	----	----	8/XI
	yes	---	-----	90°	----	----	3/XII
	no	---	-----	45°	----	----	3/I
	no	---	-----	30°	----	----	5/I
	yes	---	-----	90°	----	----	10/XII
	yes	---	-----	90°	----	----	30/XII
	yes	---	-----	50°	----	----	31/I
	yes	---	-----	90°	----	----	31/I
	yes	---	-----	90°	----	----	4/II
	yes	---	-----	75°	----	----	4/II
	yes	1.2	25.0 long 5.0 wide	20°	----	----	26/II
	no	5.0	6.5 diam	45°	5.0	180°	26/II
	yes	1.2	2.5 diam	30°	2.5	----	11/III
	no	3.7	17.5 long 5.0 wide	----	----	180°	28/III
	no***	1.2	5.0 diam	----	25.0	20°	22/V
					5.0	180°	

*m = mature

**approximate angle measured from the horizontal
 ***burrow located on open sand in Station 3 and may
 have been abandoned by L. ammonophila

TABLE 8 Continued

Age ^o Sex	Door	Chamber		Burrow		Branches		Date
		Depth (cm)	size (cu)	Length (cm)	Angle**	Length (cm)	angle**	
Gravid ♀	yes	2.5	5.0 long 3.7 wide	----	----	2.5#	-----	16/II
		7.5	15.0 long 7.5 wide					
	yes	---	-----	15.0	90°	----	-----	26/II
	no	2.5	5.0 diam	3.7	45°	10.0	180°	6/III
	yes	10.0	2.5 diam	20.0	40°	----	-----	11/III

**approximate angle measured from the horizontal

#between the two chambers

Burrow characteristics of *Lycosa ammophila*

Age* Sex	Door	Chamber		Burrow		Branches		Date
		Depth (cm)	size (cm)	Length (cm)	Angle**	Length (cm)	Angle**	
1.2 cm imm.	yes	---	-----	2.5	90°	---	---	21/XII
	yes	---	-----	1.8	90°	---	---	28/III
	no	---	-----	1.8	90°	---	---	19/V
pp	yes	---	-----	7.5	40°	12.5	10°	5/II
m	yes	3.7	10.0 diam	---	---	---	---	29/IX
	yes	6.2***	3.7 diam	2.4	90°	17.5	30°	5/II
	yes	---	-----	2.5	10°	---	---	26/II
Gravid	no	---	-----	7.5	90°	28.7 17.5	180° 180°	15/XII
	yes	2.4	6.5 diam	1.2	90°	50.0	160°	12/VI

*imm. = immature; pp = prepenultimate; m = mature

**approximate angle measured from the horizontal

***branching burrow at bottom of chamber was sealed with sand

the chamber corresponds to the production of egg sacs and females may use the area for making the egg sac, remaining with the egg sac and young after hatching; (2) the frequent occurrence of branching away from the chambers may allow spiders access to areas with different saturation deficits. Branches off of non-chambered burrows may have a similar function; (3) immature and non-reproductive mature spiders normally build non-chambered burrows of highly variable length. Side branches, more typical of penultimate females, are also variable in length.

The general nature of burrows was similar in both species; however, mature females of L. ammophila often had lengthier side branches off the chamber. These were usually horizontal and about 0.75 cm beneath the surface. The side branch of one spider ended under a clump of wire grass, a cool moist microhabitat.

One female, shown in Table 2 by the symbol ***, had a side branch from the bottom of its chamber ending 25 cm below the surface. The opening of this branch was sealed off with fresh dirt from the walls or bottom of the chamber. The function of this deep burrow in the winter in a moderately shady area is unknown.

The only suspected L. lenta burrow at Station 3 was near a marked female. As shown in Table 3 (***), the burrow had a chamber and side branches typical of mature female L. ammophila but the roof of the burrow system showed signs of an extensive cave-in. All L. ammophila burrows had solid roofs and lacked noticeable structural damage.

Home Range and Resighting Data

Of the 57 adult L. lenta females marked and released at Station 5 in 1971, only 37% (21) reappeared two or more times and 16% (9) four

or more times. Resighting values of females at Station 3 in 1970 are 35% (26) of the 75 L. ammophila and 29% (5) of the 17 L. lenta appearing two or more times. Twenty-four percent (18) of the L. ammophila reappeared four or more times. The frequency of multiple resightings of females is shown in Table 10 for L. lenta and in Table 11 for L. ammophila. The sudden disappearance of spiders with home ranges or the lack of any resightings could be the result of death, extended inactivity within the burrow or migration from the study area. The frequency of each of these events is not predictable from the data. One L. ammophila, first sighted on 14 July 1970, was not resighted until February 26, 1971; it presumably overwintered in its burrow. One L. lenta marked 26 May 1970, and resighted once near the release point appeared again 60 days later 40 m away.

Active females reappeared nearly every evening. Gaps of two or three days between resightings reflect infrequent observation as much as spider inactivity. Gaps of seven or more days are not, however, due to lack of observations. The reason or reasons for these periods of inactivity are unknown.

The mean home range sizes with 95% confidence intervals based on spiders resighted four or more times are shown in Figure 11. After examining each home range in the field, I feel that the high degree of variability in area reflects an adaptation of each spider to the character of the area around the burrow rather than to the general nature of the community where it is found. No significant correlation was noted between the weight of individuals and home range size. Lyosa ammophila did tend to have larger home ranges than L. lenta from the same station, an observation correlating with the larger average size and weight of the species.

TABLE 10

Days between resightings for *L. lepta* females with home ranges*

Initial Sighting	Days between subsequent resightings											
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
STATION 5												
21/V	6	3										
21/V	10	6	1	1								
26/V	4	15	1									
1/VI	7	1	3									
4/VI	3**	1	1									
7/VI	2	1	2	1	1	1	7	7				
9/VI	3	1	1	1	1	2	1	1	2	1	1	2
13/VI	1	1	1	3	4	1						
13/VI	3	4	3									
16/VI	2	1	1	3								
16/VI	2	2	3	7	15							
17/VI	6	2										
19/VI	4	2										
22/VI	21	1										
25/VI	4	1	14									
24/VI	19	1										
24/VI	5	1										
30/VI	5	2										
30/VI	5	1	1									
3/VII	4	6	1	1	1	4						
6/VII	2	6										
STATION 3												
3/VI	1	10	3	6	7							
4/VI	1	9	3	3								
7/VI	1	4	4	2	1	1	1	1	3	7		
9/VI	3	6	1	1	1	5	2	4				
17/VI	1	8	1									

*based on two or more resightings

**moved from previous home range

Days between resightings for *L. wyomblin* females with home ranges*

Days between subsequent resightings

Initial Sighting 1st 2nd 3rd 4th 5th 6th 7th 8th 9th 10th 11th 12th 13th 14th 15th 16th 17th

STATION 3

17/Vi	2	1	3	1	2	3	1	1	1							
17/Vi	6	1														
17/Vi	3	3	1	5	1	1	2	2	1	3	1	4	5	1	2	1
18/Vi	1	1	4	2	4	1	1	1	2	2	10**	1	3	1	3	1
18/Vi	1	1	9	2												
18/Vi	38	1														
20/Vi	9	1	1	1												
22/Vi	8	1	1	1	47											
22/Vi	21	1	2													
29/Vi	1	2	1	2	5	2	1	1	1	1	4					
31/Vi	1	1	8	3												
2/Vii	1	20**	1	2	1											
6/Vii	3	3	1	1	1	4	3									
10/Vii	3	2	1	3	1	4										
10/Vii	2	15	8													
10/Vii	3	1	1	1	3	1	2									
12/Vii	2	1	1	3	4	1										
12/Vii	1	32	1													
12/Vii	2	5	1	2	1	4	3	14								

TABLE 11 Continued

Initial Resighting	Days between subsequent resightings										
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th 12th 13th 14th 15th 16th 17th
12/VII	7	7	56**	1							
14/VII	1	5	4								
14/VII	2	3	4	3	3	5	1	7	2		
14/VII	9	20	180**	2							
16/VII	7	1**	2	1							
23/VII	4	7	1	1	7	2	2				
24/VII	3	8									

*based on two or more resightings

**moved to new home range

Figure 11. Mean home range sizes with 95% confidence intervals.
Only data for mature females resighted four or more
times were used for calculations.

Mature males of both species wander and do not, therefore, have a home range as characterized above. Of 69 male L. lenta marked at Station 5, 31% (21) were resighted once, 17% (12) twice, 4% (3) three times and only 1.5% (1) were resighted a fourth time. At Station 3, only 24% (13) of 53 L. ammophila males marked reappeared once, 7.5% (4) twice, and 2% (1) a third time. Of the 21 L. lenta males marked at Station 3, resighting consisted of 19% (4) once and only 5% (1) twice. The lower resighting frequency of both species at Station 3 may result from a lack of barriers such as the stream present in Station 5, and the large areas adjacent to the study area suitable for invasion.

No burrows harbored adult males and no males built burrows in the laboratory. It is unknown, therefore, whether males build or occupy burrows.

The infrequent resighting of males and the variable distances between resightings makes it impossible to calculate a meaningful average daily movement rate. Two noteworthy resightings include: (1) an L. lenta male moved from one side of Station 5 in two days to the other side (23.75 m), was seen in copulation, and returned at least two days later to the first side (22 m). These were the third and fourth resightings for this male within 12 days of release. He was not sighted again; (2) an L. ammophila male released in dense wire grass reappeared 12 m away one half hour later. If the spider had continued at this pace for hours, it would have moved nearly 200 m. Most males observed were not walking, however, but were standing quietly; therefore, the average nightly migration distance is probably less than 200 m.

Females occasionally move from their burrows and establish new ones; the pertinent field observations are in Table 12. The reason for the moves is unknown; however, in the few cases observed, spiders remained in the same habitat.

Since all females with young had no marks, they had presumably migrated into the study areas. Perhaps abandonment of the home range normally follows the emergence of the young from egg sac.

Distribution and Habitat Preferences

The capture localities of mature spiders and the number of home ranges in the various habitats of Stations 3 and 5 appear in Table 13. The observed densities of females and home ranges given per 1000 m² appear in Table 14. A chi-square analysis of the null hypothesis that the distribution of L. ammophila females was random using an expected density of 12.7 females/1000 m² in all habitats of Station 3 resulted in rejection at the 0.5% significance level. Similar tests for L. lenta females at Stations 3 and 5 showed that the species had a non-random distribution ($P = 0.05$).

At Station 3, densities of L. ammophila females were not highest in the turkey oak-wire grass area as might have been expected, but rather in the sandy old field area and, secondly, in the ecotone between turkey oak-wire grass and live oak hammock. This distribution holds as well for home range densities, being higher in the old field region. The disparity in density of females and home ranges between the turkey oak-wire grass and live oak habitats suggests that mature females emigrated from the former habitat soon after they entered or, in the case of residents, soon after emerging from the penultimate moult (discussion of immatures follows). This idea is

TABLE 12

Known movements of mature females from one home range* to another

Species	Station	Time between sightings (days)	Distance moved (m)**
<u>ammophila</u>	3	56	20
<u>ammophila</u>	3	10	3.5
<u>ammophila</u>	3	20	20
<u>ammophila</u>	3	180	14
<u>ammophila</u>	3	1	10
<u>leata</u>	3	1	2.6

*based on two or more resightings

**from last resighting in first home-range to first resighting in second. The second and sixth spiders were resighted over four times in both homeranges.

TABLE 13

Habitat distributions of mature spiders at capture points in 1970

Station	Habitat	<i>Lycosa annuophila</i>		<i>Lycosa lenta</i>	
		males	females home ranges*	males	females home ranges*
3	turkey oak-wire grass (a)	24	33	13	3
	old field (b)	4	15	3	0
	live oak (c)	19	11	4	3
	grass (d)	1	4	1	0
	road (e)	2	6	3	0
5	annual weed (a)	-	-	-	4
	grass and leaf litter (b)	-	-	41	43
					20

*based on spiders resighted at least twice within a distance of 3 m or less

TABLE 14

Observed density of marked spiders and home ranges per 1000 m² in 1970

Station	Habitat	<u>Lycosa ammophila</u>		<u>Lycosa lenta</u>	
		Home Ranges*	Females	Home Ranges*	Females
3	turkey oak-wire grass (a)	4.2	10.8	0.9	1.3
	old field (b)	26.6	50.0	0.0	0.0
	live oak (c)	11.4	28.6	8.5	22.9
	grass (d)	0.8	3.3	0.0	0.8
	road (e)	6.0	12.0	0.0	0.0
5	annual weed (a)	-	-	2.1	6.3
	grass and leaf litter (b)	-	-	12.5	26.9

*based on spiders with two or more resightings

supported by the observations that high densities occurred at the borders of this habitat and that unmarked females in wire grass were almost always moving when sighted. Females moving into the edge of the live oak hammock occasionally established home ranges; those moving into the old field region did so more frequently. The extreme density of the wire grass and the relative paucity of open sandy spaces in habitat "a" (Figure 1a) is probably a major factor influencing this distribution. In other regions adjacent to Station 3 and in Stations 1 and 2, where wire grass was sparse and open sandy spaces common, mature L. ammophila females were more abundant; they were found most frequently on the open sandy patches between leaf drifts. The higher density of females and home ranges in the hazardous "road habitat" again reflects the species' preference for open sandy areas.

L. lenta females at Station 3 were almost exclusively in the live oak ecotone. Those with home ranges in the turkey oak-wire grass habitat were under fairly dense stands of 3 to 4 m tall turkey oaks where leaf litter had begun to accumulate in and between mats of wire grass. Females of the species were not in unshaded or open sandy areas and rarely occurred in tall grass.

The males of the two species moved through all habitats at Station 3. Lycosa ammophila males were abundant in the ecotone with the live oak but rarely entered the live oak habitat. The high frequency of nonresidents at this site suggests an ecological barrier effect where individuals accumulate before returning to the turkey oak-wire grass or old field habitats. I observed L. lenta males outside the live oak hammock infrequently; the frequency of their occurrence in the more xeric habitats correlated roughly with the area of the habitats.

The distribution of L. lenta males and females at Station 5 correlates very well with the presence of scattered low grasses and well-mulched leaf litter and the absence of tall dense weeds. The difference in numbers was four to one, and in home range densities, six to one.

Immatures of L. ammophila in all stations where the species occurred were found in association with leaf litter and wire grass and were uncommon on open sand. All of the borrows of immature spiders were in or very near leaf litter or wire grass. These microhabitats, besides being more moderate in temperature and moisture fluctuations, afford a degree of isolation and protection from larger predaceous spiders.

The results of the 1971 study at Station 6 (Table 15) again demonstrated L. ammophila's preference for open lightly shaded sandy areas while L. lenta prefers shaded areas with leaf litter or mulch and few dense grasses or weeds. When given the choice of six fairly distinct habitats, both species avoided habitat "a" (Figure 2) with its low dense weeds. In habitat "b", however, differing from "a" by its lack of dense weeds and the presence of extensive broadleaf and pine needle litter, L. lenta frequently became established following release. Thirty-five percent (7) of the marked females reappeared with home ranges, all within a 5 m radius of the release points. Only 5% (1) of the L. ammophila females developed a home range. This individual was ca. 40 m from its release point. The other L. ammophila females were resighted 16 to 50 m from the release point. Two L. ammophila females and one male were resighted in habitat "c" and had migrated from the release point in "b". No marked L. lenta were in the grass of habitat "c".

Migration and distribution of marked mature L. lentis and L. ammophila one month or more after release at one of six habitats within Station 6.

Habitat	Total <u>L. lentis</u> released	Total resighted	Release point habitat	No. of		Total <u>L. amm.</u> released	Total resighted	Release point habitat	No. of	
				Home ranges*	H. R./♀♀ released				Home ranges*	H. R./♀♀ released
a) heavy shade; low dense weed	0	0	-	-	-	0	0	-	-	-
b) heavy shade; leaf litter	14♀ 8♂	7♀ 3♂	b b	5 (35%) -	-	20♀ 12♂	5♀ 3♂	b b	1 (5%) -	-
c) unshaded dense lawn	0	0	-	-	-	0♀ 0♂	2♀ 1♂	b b	0 -	0 -
d) light shade, patchy lawn	64♀ 42♂	12♀ 2♂	11-d, 1-f d	4** (6%) -	-	46♀ 26♂	9♀ 1♂	8-d, 1-f e	6 (13%) -	-
e) heavy shade; tall grass	9♀ 5♂	3♀ 0♂	1-d, 2-f -	0 -	0	1♀ 1♂	0♀ 0♂	- -	0 -	0 -
f) moderate shade, leaf litter	8♀ 0♂	4♀ 2♂	f d	3 (37%) -	-	6♀ 1♂	2♀ 0♂	f -	0 -	0 -

*based on two or more sightings within 3 m or less

**3 of the four located in heavy leaf litter under bushes

On the other side of the stream, L. lenta showed a small tendency to remain in habitat "d" following release. Only 6% (4) were in home ranges and all of these were in microhabitats with well-shaded leaf litter. L. ammophila, however, established in this habitat most frequently. Of six home ranges, 4 were in microhabitats with scattered patches of sand in light to moderately shaded areas. Two of the six home ranges represented females having emigrated from habitats "e" and "f". It is important to note that six unmarked mature females of L. ammophila appeared during the late spring and early summer near the release point in habitat "c". Penultimate females were released earlier in the year and were frequently resighted, indicating L. ammophila can undergo the final moult to maturity in a "mesic" habitat.

Neither species became established in habitat "e" with its tall grasses and few unmarked L. lenta were ever seen there. Habitat "f" was apparently quite suitable for L. lenta, since three of eight females there established home ranges. This habitat had moderate to heavy shade and extensive regions of leaf litter similar to habitat "b", the pine woods.

Of the 58 L. lenta females marked and released in an open-sand turkey oak-wire grass habitat near Station 3 in 1971, eleven re-appeared at least once, three twice and only one three times. Seven resightings were within 3 m of the release point and the spiders survived from 30 to 60 days. The remaining four were seen from 8 to 20 meters away; one had lived 20 days, the others 105, 107 and 108 days. Although 54 unmarked immatures were released, no unmarked adults were collected in the area and very few immatures were seen more than a few weeks following release.

The L. lenta female placed in the cage on unshaded open sand lived 63 days, from February to April. It was resighted regularly before being destroyed during construction activities in the area. This observation and the data for unconfined marked females in the same habitat support the conclusion that mature L. lenta can survive in the harshest areas where L. ammophila normally occur but typically avoid these areas. Any L. lenta burrowing in such areas would experience increasing thermal stress as summer arrived, a situation absent in their more normal shaded mesic habitat.

DISCUSSION

Evolution of the Species

A review of the current theories of geological events in the South-eastern United States during the Quaternary reveals L. ammophila had ample time and the necessary isolation to adapt to the sandhill community. A submersion of Florida existed during the Oligocene when spiders were undergoing adaptive radiation and the first lycosids appear in the fossil record. Perhaps as early as the Late Miocene the sea level dropped exposing the peninsula to invasion from the mainland (Alt and Brooks, 1964; S. D. Webb, personal communication). Laessle (1968) reports evidence that some modern sandhill communities (longleaf pine-turkey oak) have existed essentially unchanged since Pliocene or Late Miocene; consequently, the presence of stocks of the L. ammophila precursor was possible. The precursor was likely L. lenta or some common ancestor since the two species are so similar in morphology and reproductive behavior.

During the first clearly recognized interglacial period, sea level rose 45 m to the Okefenokee shoreline, isolating several islands and island groups (MacNeil, 1959; McCrone, 1963). Only the highest hilltops of the oldest areas of modern Florida were exposed. These areas supported primarily sandhill associations due to their eroded, well-drained, sandy nature. The small number of plant species typical of the association resulted not only from poor moisture-holding characteristics and infertility of the soil due to leaching but also

from fires which prevented the community from undergoing succession through xeric hammock to mesic hammock (Laessle, 1958, 1968; A. Carr, personal communication). The present distribution of the species suggests that L. ammophila evolved on one or more of the northern-most islands.

Three other known glacial periods occurred during the Pliocene and Pleistocene. During each interglacial, sea level rose to a lower level than in the one previous. During the first, it rose to the 30 m level, again isolating numerous islands. Nearly all the current sandhill communities were established on the lower wave-eroded hill-tops exposed during this interglacial. If speciation of L. ammophila did not occur during the previous interglacial, a second chance occurred.

During the final two interglacials, northern and central Florida were not inundated and extensive mesic areas surrounded the sandhill communities. Presumably, L. lenta occupied many of these mesic areas and has maintained his distribution pattern without successfully colonizing the sandhill communities. The change in pheromones may have occurred during isolation or when the species came into contact.

Numerous other examples of speciation during the Late Quaternary in Florida have been documented. They include studies of the wolf spiders of the Geolycosa pikei complex (McCrone, 1963), beetles of genus Mycotrupes (Hubbell, 1954), grasshoppers of the Melanopus puer complex (Hubbell, 1932, 1956) and snakes of the genus Stilosoma (Highton, 1956).

The niches of L. ammophila and L. lenta

One of the major adaptations of L. ammophila to the sandhill community is the limitation of reproduction and general activity to

the wet summer months (Figures 4 and 7). During this period, the climate is most moderate and survival of the young is apparently maximized. Mature spiders are uncommon during other seasons when rainfall is infrequent and inconsistent, daily temperature fluctuations are large, evening temperatures cool and the habitat less mesic (Figure 12); younger instars are infrequently active, remaining in their burrows many evenings. In contrast, L. lenta breeds from late winter to early autumn and the younger instars are active on any warm, humid evening. The difference is correlated with the presence of a daily and seasonally moderated microclimate in the shaded mesic habitat.

A further adaptation of L. ammophila to seasonal quiescence is an increase in life span to two years (Figure 12). Recognition of specific life stages in the field is much easier for L. ammophila any given month than for L. lenta populations; the overlap of life stages of L. lenta results from the prolonged breeding period. Lycosa lenta populations may be resolved into spring and summer generations upon further study; it appears, however, that most spiders reach maturity in one year. The life cycle of the L. lenta population at Station 3 was in phase with those at Stations 5 and 6, suggesting endogenous control. Similar data for L. ammophila populations are lacking.

Lycosa ammophila has several characteristics better adapting it to xeric environments than L. lenta. First, in moderately dry test environments, the percent weight loss per hour of L. ammophila is lower than that of L. lenta of equal weight (Figure 9, Table 6). The mechanism of water retention remains to be identified. The

Figure 12. Proposed life cycles for Lycosa ammophila and L. lenta in north-central Florida. The width of the bars indicates only the relative abundance within each age class. Dashed lines indicate areas which, for lack of sufficient data, are not accurately resolved. No L. ammophila females with egg sacs were seen in the field. One mature female (*) survived in the field to the next spring; it is unknown whether she would have bred if left undisturbed. Abundance of males is approximately equal to that of females throughout. The species probably have ten instars (Whitcomb, 1967).

advantage in survival time is small but is correlated with the inactivity pattern of L. ammophila during dry seasons. Second, the average weight of mature L. ammophila is larger than that of mature L. lenta (Table 3), allowing them to tolerate dessication longer before drinking.

Although the resting metabolic rates of well-fed spiders are identical, incomplete preliminary studies of fasting spiders suggest that L. ammophila may undergo a greater reduction of resting metabolic rate than L. lenta. This increased energy conservation would allow L. ammophila to feed less frequently, e.g., when inactive within the burrow. This would be a third adaptation of L. ammophila to the sandhill community.

Other physiological characteristics determined for the species, critical thermal maxima (Table 7) and the temperature of suspected cuticular wax disruption (Figure 10), were essentially identical. Lycosa ammophila shows no differential adaptation with respect to these factors to a xeric environment. In addition, neither species showed any significantly different behavioral responses when heated (Table 7).

The water loss rates of L. ammophila and L. lenta, compared with rates for other arachnids (Table 16), are higher than most xeric-adapted species which have been studied. Reasonably accurate comparisons are possible if the data are adjusted to constant saturation deficits (e.g., 3.3X for the desert scorpion Hadrurus arizonensis) and the rate of water loss for L. lenta and L. ammophila increased accordingly (e.g., $3 \times 0.144 = 0.428$ percent weight loss per hour for L. lenta at 30°C , 0% R.H.). A 1.0 g H. arizonensis would

Water loss comparison in xeric adapted arachnids with Lycosa lenta and Lycosa amophila.

Species	weight (g)	Temp. (°C)	Rel Hum. (%)	Sat. Def. (mm Hg)	% wt. loss per hour	Source
SPIDERS						
<u>L. lenta</u>	1.0	25	55	10.5	0.144	This study
<u>L. amophila</u>	1.0	25	55	10.5	0.120	This study
<u>Dugesiella bentzi</u>	11.04 - 12.65	35	dry	35.8	0.13 - 0.14	Stewart and Martin (1970)
<u>Euryvelva</u> sp.	-	33	0	37.7	0.147	Cloudsley-Thompson (1967)
<u>E. helio</u>	ca. 12	25	25	17.6	0.60	Herreid (1969)
<u>E. californicum</u>	ca. 12	25	25	17.6	0.45	Herreid (1969)
SUN SCORPIONS						
<u>Galeodes granti</u>	-	33	0	37.7	0.09	Cloudsley-Thompson (1967)
WHIPSCORPIONS						
<u>Nasitigroproctus giganteus</u>	ca. 3	30	0	31.8	0.300	Ahearn (1970)
<u>Nasitigroproctus arizonensis</u>	1.0	30	0	31.8	0.750	Ahearn (1970)
SCORPIONS						
<u>Centruroides sculpturatus</u>	-	30	0	31.8	0.091	Hadley (1970)
<u>Diplocephrus</u> sp.	-	30	0	31.8	0.044	Hadley (1970)
<u>Hadrurus arizonensis</u>	5.0 - 7.0	30	0	31.8	0.028	Hadley (1970)
<u>Hadrurus arizonensis</u>	1.0	30	0	31.8	0.07	Hadley (1970)

lose about one-fifth and one-sixth as much body water per hour as 1.0 g L. ammophila and L. lenta, respectively, at 30°C, 0% R.H. A 1.0 g whipscorpion, Mastigoproctus, would lose 1.75 and 2.0 times as much body water as 1.0 g L. ammophila and L. lenta, respectively. Mastigoproctus, studied in Arizona, is less efficient at physiological water conservation than either of the lycosids. It avoids rapid dessication by burrowing beneath rocks and logs, and is even found in semi-mesic areas of Florida. Unfortunately, data for 1.0 g hunting spiders is not available and comparisons with 12.0 g spiders may be invalid.

The sparse data available for critical thermal maxima and temperatures of suspected cuticular wax disruption of other arachnids (Table 17) show that L. ammophila and L. lenta have higher tolerances than any Scandinavian lycosids studied. Tolerances are lower than that of the desert scorpion. These comparisons support the conclusion that L. ammophila is nearly as mesically adapted as L. lenta. Lycosa ammophila does not possess physiological adaptations sufficient for water conservation in a continuously xeric microclimate.

Burrows provide concealment from predators and help in the maintenance of an optimal microclimate when conditions on the surface restrict activity. The latter factor is more important for L. ammophila in the sandhill community than for L. lenta in more mesic areas. When summer surface temperatures reach over 60°C, L. ammophila must burrow at least 3 cm deep to avoid heating above the critical thermal maximum, at least 5.5 cm to avoid the suspected cuticular wax disruption, and at least 6 to 6.5 cm to reach a maximum daily temperature which is behaviorally acceptable (Tables 1 and 7).

Species	Habitat	Cuticular wax disruption (°C)	Critical thermal maximum (°C)	Source
SPIDERS				
<u>Lycosa latida</u>	S. E. U.S.A. mesic	ca. 38	48	This study
<u>L. amplexilla</u>	S. E. U.S.A. sandhills	ca. 38	48	This study
<u>L. pulchra</u>	Denmark sphagnum bog	-	35.3	Nørgaard (1951)
<u>Pardosa piraticus</u>	Denmark sphagnum bog	-	43.0	Nørgaard (1951)
<u>L. nigriceps</u>	S. Sweden dunes	-	39.7	Almqvist (1970)
<u>Zelotes serotinus</u> (Gnaphosidae)	S. Sweden dunes	-	46.4	Almqvist (1970)
<u>Dugesiella hentzi</u>	Texas	ca. 38	39	Stewart and Martin (1970)
WHIPSCORPIONS				
<u>Mastiprionotus giganteus</u>	Chiricahua Mts. Arizona	37.5	-	Ahearn (1973)
SCORPIONS				
<u>Hadrurus arizonensis</u>	Phoenix, Arizona	ca. 38 and 65	70?	Hadley (1970)

*temperature where rate of water loss sharply increases.

Temperature regulation may be possible for mature spiders by moving along the side branches typical of the burrows located. Small instars of L. ammophila burrow in areas of wire grass and leaf litter and need not dig as deep to avoid high temperatures (Table 1). During winter and spring when L. ammophila is least active, energy and water conservation could be maximized if the burrow were about 17.5 cm deep, the depth where the lowest constant temperature occurs (Table 2). One burrow found was nearly 50 cm deep; it is not possible to say whether or not deep winter burrows are characteristic of the species.

The major similarity between summer burrows of mature L. lenta and L. ammophila females is the shallow chamber, presumably serving as an area for the production and carrying of the egg sac and newly emerged young. In the sandhill community, the shallow chambers probably heat to 30 to 40°C or more in the afternoon (Table 2), hypothetically requiring the females to move the egg sacs to cooler areas of the burrow system. Behavioral thermoregulation of the egg sac has been demonstrated for an orb weaver, Theridion saxatile (Nørgaard, 1956) and a wolf spider, Pirata piraticus (Nørgaard, 1951). It is conceivable that the optimum temperature for development of the eggs of L. ammophila may be higher than that for L. lenta eggs, and that L. ammophila females can reduce their resting metabolism even lower than the 20% compensation by L. lenta when changed from 20°C acclimation to 30°C demonstrated by Anderson (1970). This would allow mother and egg sac to survive in or near the heated chamber without increasing energy requirements unduly. These speculations suggest further lines of investigation.

Several factors in addition to reduced water loss relate to the larger size of L. ammophila. The primary selective force for increased

leg and cephalothorax dimensions may have been the need to support a large abdomen, the region of water and energy storage. The increase of size hypothetically places mature L. ammophila in a different feeding niche than L. lenta, although data from this study do not show any significant difference (Tables 4 and 5). It is apparent, however, that in encounters between mature spiders, L. ammophila would eventually eliminate L. lenta. This effect was demonstrated at Station 6 when L. ammophila was released into the habitat of L. lenta (Table 4).

Another factor involved with increase in body size of L. ammophila is the requirement for more food. The larger average home range size of the species as compared to that of L. lenta studied in the same habitats supports this speculation (Figure 11). Adaptations in energy conservation may have reduced the need for even larger home ranges for L. ammophila. In the only study of home ranges in southeastern United States lycosids, Kuenzler (1958) studied L. timuqua, the member of the lenta complex replacing L. ammophila in the Florida scrub community and in the longleaf pine-turkey oak community from Georgia north to Virginia. He reported a mean home range size of 9.2 m^2 (103 ft²) for a population in South Carolina, a value considerably larger than that of either species examined in this study. The difference may be a response to the local climate; a Florida population should be studied before attempting further comparisons.

The larger average size of mature spiders in the lenta group compared to smaller lycosids makes the spiders of the lenta group ill-adapted to a climbing mode of foraging. This restriction affects L. ammophila more than L. lenta and in part explains their habitat distributions and preferences. Hallander (1967) used this same

reasoning in explaining the nearly allopatric distributions of Pardosa chelata and P. pullata in Sweden. In the case of L. ammophila, the large mass and long legs of the larger instars may prevent them from moving with any degree of agility over wire grass or through other types of dense vegetation. This may apply as well to unstable surfaces like leaf litter, with the result that foraging success, and reproductive success, is greater for those individuals establishing home ranges on open surfaces. This correlates with the observation that large instars of L. ammophila migrate away from wire grass and leaf litter to more open areas. Determination of the influence of genetic control on habitat selection will require more controlled habitat choice studies in the field and laboratory.

Lycosa lenta, as a result of its smaller size compared to L. ammophila, may forage more successfully on leaf litter and in sparse vegetation. With the exception of about 5 to 20% of the mature females in the population studied, the species does not occur in dense vegetation. Foraging efficiency is perhaps so low that migrating spiders do not linger in these areas. The absence, by early summer, of larger instars of L. lenta from the open sandy areas of Station 6 correlates not only with the increasing presence of large L. ammophila but also with increasing afternoon temperatures. The L. lenta released at Station 3 in late winter and early spring when L. ammophila was quiescent also failed to become established, perhaps in response to high, fluctuating temperatures. The effect of physical parameters on the survival and habitat preferences of L. lenta needs further study.

Differential survivorship of the small instars of the species in each of the two habitat types might be a factor reinforcing allopatry; habitat preference and selection by the young might also contribute to the mutually exclusive ranges of the species. More intensive study is required to determine the biology of the young and its effect on the distribution of the species.

In summary, it appears that L. ammophila can be viewed as a mesic species, like L. lenta, which has adapted to a seasonally xeric environment primarily by restricting activity and reproduction to the wet summer months. Some physiological adjustments to reducing water loss have been made, although they are much less effective than those of most desert arachnids. Spiders remain in sealed burrows to reduce water loss and energy expenditure during dry or cold periods.

SUMMARY

In this study, a number of behavioral, morphological and physiological characteristics of Lycosa lenta and L. ammophila were defined to allow a tentative explanation of their allopatric distribution.

The primary conclusions from this study were:

1. The macroclimates in each of the habitats where the species occur are markedly different during the day. Due to the sparse shade and poor water-retaining capacity of the sandy soil, the longleaf pine-turkey oak habitat of L. ammophila has surface temperatures as much as 25°C higher than the well-shaded mesic areas with heavy leaf litter where L. lenta is found.

2. At night, the surface temperature is several °C cooler in the longleaf pine-turkey oak community than in the mesic community. The air is saturated in both communities except in the former during periods of drought, common in autumn and winter.

3. Lycosa ammophila's reproductive peak coincides with the months of greatest rainfall (June, July and August) while L. lenta is reproductively active in the winter and spring as well as the summer.

4. The species are reproductively isolated, seemingly due to species specific chemical cues (pheromones) on the dragline silk of females and/or on the bodies of potential mates. The courtship patterns appear to be identical for both species, confirming a close relationship.

5. Lycosa ammophila females are significantly larger than L. lenta females, based on cephalothorax dimensions, leg lengths and, during

reproductive periods, weights. Mean weights of L. ammophila males are significantly larger than those of L. lenta males. Mature L. ammophila can subdue larger prey than L. lenta. Prey may include mature L. lenta females, resulting in the competitive exclusion of L. lenta from the range of L. ammophila.

6. An increase in average life span to two years appears to have occurred for L. ammophila as an adaptation to a hostile macroclimate in its habitat. The relative constancy of temperature and moisture in the mesic environment allows L. lenta to remain active nearly all year long, resulting in the retention of a one or one and one half-year life cycle.

7. Rates of water loss increase with decreasing weight for both species. Percent weight loss per hour shows an inverse relationship with body size. When held at 35°C, $90 \pm 5\%$ relative humidity without free water, a 1.0 g L. ammophila could survive about 1.8 days longer than a 1.0 g L. lenta. It is suggested that the reduction of percent weight loss per hour associated with increasing weight was the main selective advantage resulting in the larger size of L. ammophila.

8. The species are nearly identical in their thermoregulatory behavior and their physiological responses to heating to the critical thermal maximum. First behavioral responses occurred at about 36.5°C and heat death (final paralysis) at about 46°C. Acclimation to 30°C did not produce significant changes in responses from those elicited from spiders acclimated to 20°C.

9. An increase in the rate of water loss occurs at about 38°C in large instars of both species. The change is irreversible, suggesting a disruption of the orientation of cuticular wax molecules. Per-

cent weight loss per hour at 25°C, $55 \pm 5\%$ relative humidity of individuals previously heated above 38°C is about twice that of the control group.

10. Members of both species, except mature males, occupy burrows with silken doors during the day. Mature females construct a chamber about 5 to 6 cm in diameter 1 to 5 cm below the surface where they presumably make and hold the egg sac and where the young hatch. Summer L. ammophila burrows frequently have lengthy side branches 6 to 8 cm deep. During other seasons L. ammophila often remains in burrows for extended periods of time, thereby avoiding activity when the environment is most xeric. Seasonal inactivity appears to be the major adaptation of L. ammophila to the sandhill community.

11. Home range sizes were similar in the two species, about 2.5 m², with those of L. ammophila larger than those of L. lenta from the same station.

12. Both in the normal habitat, and when moved to a mesic community, mature L. ammophila females most often established home ranges in open, poorly shaded, sandy areas. Areas with dense weeds or grass or with shaded leaf litter were avoided. This habitat selection correlates with an increase in hunting efficiency for the larger species and may be genetically controlled. Lycosa lenta do not occur in areas with dense tall grass or in open sandy areas, especially when L. ammophila is present.

13. The hypothetical evolutionary history of the species is reconstructed.

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BIOGRAPHICAL SKETCH

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This dissertation was submitted to the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1971

Dean, Graduate School

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F. C. Johnson, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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