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PARAMETERS AFFECTING THE HABITAT CHOICE OF A DESERT WOLF SPIDER, *LYCOSA SANTRITA* CHAMBERLIN AND IVIE

Ann E. Kronk[1] **and Susan E. Riechert**

Zoology Department, University of Tennessee
Knoxville, Tennessee 37916

ABSTRACT

1. This study discusses a complex habitat selection strategy exhibited by a hunting spider species, the wolf spider *Lycosa santrita*, occupying desert riparian habitats in southeastern Arizona.

2. Field censuses of spider activity on various substrates show that significant associations exist between spiders and grass. This substrate provides the most predictable energy investment in prey capture of all natural substrates in the study area.

3. Mature spiders show less association with grass than younger spiders. Upon maturing, females move from the woodland area where grass is prominent to patches of bare ground and rock bordering a creek. Adult males also leave the woodland and settle in patches of leaf litter adjacent to the creek bed.

4. Available prey is shown to be highest on the bare ground substrate. As prey numbers were not found to differ significantly on any substrate through time, location changes made by adult spiders cannot be a reflection of temporal changes in local prey abundance.

5. We conclude that mature females require the greater numbers of prey afforded by the bare ground substrate for reproduction.

6. Mature male spiders move to the area of the creek bed in response to the presence of females in the area. Here the probability of mating is highest.

INTRODUCTION

To be a successful contender for resources an organism must employ a strategy which takes it to maturity and supplies its offspring with sufficient energy to initially compete for resources. One aspect of such a strategy is habitat selection which has been demonstrated to affect the fitness of spiders in various ways. For instance, it is considered by several workers to reduce interspecific competition within spider communities (Luczak 1966, Kessler-Geschiere 1971, Tretzel 1955, Gertsch and Riechert 1976, Post and Riechert 1977). Spiders have also been shown to escape thermal stress and maximize time for feeding activity by the selection of favorable microenvironments (Riechert and Tracy 1975, Riechert 1976).

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[1] Graduate Program Ecology.

Few studies have dealt with habitat selection in the more active hunting spider species. An important contribution has been made by Greenquist and Rovner (1976) who showed that two temperate wolf spiders (Lycosidae) exhibit stratum preferences. The present study was instigated by field observations of a desert wolf spider, *Lycosa santrita* Chamberlin and Ivie. These observations suggested that this spider might utilize natural substrates which enhance its hunting activities. The study reported here was initiated to test this hypothesis and to determine whether *L. santrita* might also be maximizing its prey capture efficiency through selection of favorable substrates.

LYCOSA SANTRITA

Lycosa santrita is a prominent member of the spider communities of creek bank habitats in the Chiricahua Mountains of southeastern Arizona. This large wolf spider (16-20 mm in length), like most lycosids, does not build a web trap. Prey are detected visually and through vibrations monitored by tarsal slit organs and trichobothria (Barth 1967, Gorner and Andrews 1969). Further, prey is subdued without the use of silk. *L. santrita* remains stationary while locating prey and can be considered a sit-and-wait or ambush predator. In this respect, it is similar to those spiders which utilize webs in capturing prey.

STUDY AREA

The study was conducted in a desert riparian habitat on the grounds of the Southwestern Research Station of the American Museum of Natural History, Cochise Co., Arizona. The creek traversing this habitat has running water throughout the year. Mottled shade is provided by *Platanus wrightii* (Arizona sycamore) and *Acer negundo* (box elder); the floor of this woodland is predominantly grass. A more complete description of the vegetation of desert riparian habitats is available in Lowe (1972).

CAPTURE EFFICIENCY

Optimal foraging includes parameters related to: 1) food choice, 2) patch choice, 3) time allocation between different patches and 4) patterns and speed of movement (Pyke et al. 1977). We are concerned here with patch choice (i.e., the possibility that spiders might limit their hunting activities to specific substrates).

Although animals commonly select "patch" types according to the prey they offer (kinds and numbers), few examples of patch choice based on capture efficiency are available (See for example Bell 1971, Greenquish and Rovner 1976). The following experiment was designed to determine what effect, if any, substrate has on the capture success of *L. santrita*.

Methods.—Feeding experiments were conducted in plexiglass boxes (34.5 x 35 x 15.5 cm) each containing a different substrate type (i.e., rock, leaf litter, grass, or bare ground). (Grasshoppers are favored prey of this species population). Spiders chosen for a specific run had not been fed for at least 3 days.

Ten replicates were run for each substrate type using a total of 13 female and 15 male spiders. Two estimates of capture efficiency measured in the experiment were: 1) distance between the spider and the prey at the time of spider orientation towards the prey, and 2) the time between spider orientation and actual prey capture. In addition to substrate the following factors were measured for each run: the size of the spider relative to that of the prey, resting heart rate of the spider and its temperature. Total body length and anterior width were used as a size estimate for prey, and cephalothorax and abdomen lengths and widths were used as spider size estimates; these were measured with a millimeter rule. Heart rate was estimated via the laser-illumination method described in Carrel and Heathcote (1976), and spider temperature was assumed to be equivalent to air temperature within the chamber (Riechert and Tracy 1975).

Results.—Once a spider detected, oriented towards, and then jumped forward to a prey in the experiments, it was always successful in the capture of that prey regardless of the substrate provided. Before considering the effects of substrate on the spider's ability to detect prey or on its capture time, it was necessary to correct the data for confounding by the various covariates listed above. Thus, analyses of covariance with multiple covariates (Bennett and Franklin 1954) were applied to the data (Table 1). A Duncan's multiple range test (Snedecor and Cochran 1967) was then used to test for differences existing among the substrates in corrected mean values of both distance and time (Table 2).

Table 1a.—Covariate statistics related to error within distance treatments. (r = regression coefficent, SE = standard error, t = t-value).

Covariate	r	SE	t	Tabular t
CEW	-3.3283	7.7409	-0.4300	$t_{(35,0.2)}=0.85$
CEL	6.1004	5.1407	1.1867	$t_{(35,0.1)}=1.31$
ABW	-12.7210	6.8594	-1.8584	
ABL	2.4140	4.9856	0.4842	
PRW	-11.6497	12.1564	-0.9583	$t_{(35,0.2)}=0.85$
PRL	1.6844	2.4844	0.6780	$t_{(35,0.3)}=0.53$
TEMP	-0.1859	0.6840	-0.2717	
HTBT	-0.0656	0.2257	-0.2905	
DOFI	0.0315	0.6868	0.0459	
DWFD	0.0585	0.7482	-0.0782	

Table 1b.—Covariate Statistics Related to Error within Latency Treatments (CEW = cephalothorax width, CEL = cephalothorax length, ABW = abdomen width, ABL = abdomen length, PWR = prey anterior width, PRL = prey length, TEMP = air temperature at time of capture, HTBT = resting heart rate of spider, DOFI = number of days since capture, DWFD = number of days since last feeding).

Covariate	r	SE	t	Tabular t
CEW	54.4964	79.8977	0.6821	$t_{(35,0.3)}=0.53$
CEL	7.7716	53.0598	0.1465	
ABW	-8.3161	70.7993	-0.1175	
ABL	-21.1121	51.4592	-0.4103	
PRW	-106.3960	125.4729	-0.8480	$t_{(35,0.3)}=0.53$
PRL	6.0850	25.6431	0.2373	
TEMP	7.8239	7.0509	1.1082	$t_{(35,0.2)}=0.85$
HTBT	-2.5939	2.3297	-1.1134	$t_{(35,0.2)}=0.85$
DOFI	-5.6180	7.0886	-0.7925	$t_{(35,0.3)}=0.53$
DWFD	-5.7729	7.7226	-0.7475	$t_{(35,0.3)}=0.53$

Table 2.–Results of Multiple Range Tests [Underlined values are not significantly different from each other ($P > 0.05$)].

a. For Adjusted Orientation Distance:

	Substrates			
Statistic	Grass	Rock	Litter	Bare Ground
Adjusted Treatment $\bar{X}$ (mm)	51.1	42.1	41.0	40.5

b. For Adjusted Time:

Statistic	Grass	Rock	Litter	Bare Ground
Adjusted Treatment $\bar{X}$ (sec)	25.4	71.1	90.8	254.8

Substrate was not found to significantly affect either the spider's ability to detect prey at certain distances nor its capture time. However, significant correlations were observed in the relationship existing between detection distance and capture time (Table 3). This relationship can be considered a reflection of predictability of energy investment– the more linear the relationship, the more predictable is energy expenditure. The grass substrate exhibited the greatest linearity between detection distance and capture time, though significant correlations were also exhibited by leaf litter and rock (Table 3). Bare ground demonstrated a very poor correlation between the two parameters.

SUBSTRATE ASSOCIATIONS

Since grass substrates provide *L. santrita* significantly greater prey capture efficiency than other substrates, one would expect this spider to exhibit a preference towards them. Testing for active choice, however, is a problem because wandering spiders do not occupy specific sites for any length of time: individual spiders are difficult to locate and to follow. Our observations of *L. santrita* in the field indicate this spider to be basically a sit-and-wait predator. Unlike members of the genus *Pardosa, L. santrita* does not frequently move up and down grass stems in search of prey. Rather movements by *L. santrita* result in changes in habitat position. Greenquist and Rovner (1976) avoided the problem by limiting their work on stratum choice of *Lycosa* and *Schizocosa* to artificial substrates in laboratory cages, though Edgar (1971) has studied the seasonal movements of *(Pardosa) lugubris* in the natural habitat. We attempted to study habitat choice in the field with natural populations.

Methods.–The association of *L. santrita* with specific substrates in the study area was determined through field censusing of spider activity. Five adjacent quadrats (30 m long and 1 m wide) were laid parallel to the creek bed. These were sampled at random with two

Table 3.–Correlation Coefficients Showing the Significance of Linear Relationships between Distance at Orientation and Capture Time for different substrates.

Substrate	r	Tabular r
Grass	0.9428	$r_{0.001(8)}=0.8721$
Rock	0.6836	$r_{0.05(8)}=0.6319$
Leaf Litter	0.6824	$r_{0.05(8)}=0.6319$
Bare Ground	0.6177	not significant

constraints: 1) that each quadrat was examined once a day and 2) that all quadrats were sampled once in a 5 day period at each of the following times: 0600, 0900, 1300, 1700 and 1900 hours. A census consisted of a one minute examination of each square meter of a quadrat for spider presence. Substrate type, location of the square meter within the quadrat, sex of the spider and activity at the time of observation were recorded for all sightings. These censuses were conducted over a 21 day period in August and September 1975.

The representation of different substrate types in the habitat was assessed through use of cover estimates made within the same quadrats used in the activity censuses. A gridded, plexiglass sheet was placed over each meter and the number of 20 x 20 cm squares occupied by each of the substrates (rock, bare ground, leaf litter and grass) was tallied.

Results.–While censusing spider activity, we found habitat associations to vary with time, coinciding with the maturation state of the spiders. For this reason, the analyses reported here were performed on subsamples consisting of individuals of similar age and sex.

Using the frequency representation of substrate cover scores as the expected, the association of spiders with specific substrates was tested for by application of chi square tests (Snedecor and Cochran 1967). Grass was found to be the only substrate with which the spiders exhibited significant associations. Penultimate spiders demonstrated the greatest positive association with this substrate (P - females: $X^2 = 20.6$, $P < 0.005$; P - males: $X^2 = 10.6$, $P < 0.005$); adult females exhibited less association ($X^2 = 7.0$, $P < 0.01$) and males exhibited the least significant association ($X^2 = 5.3$, $P < 0.025$). A look at the activity of the various age and sex classes of spiders on the substrates explains the decrease in association noted with age (Fig. 1). Mature females appear to utilize patches containing bare ground and rock to a greater extent than younger females, while adult males show greater activity in areas containing more bare ground and leaf litter. Differences in substrate association existing between younger spiders and adults are significant (P - female with Ad - female: $X^2 = 18.1$, $P < 0.005$; P - male with Ad - male; $X^2 = 19.6$, $P < 0.005$). No significant differences were found to exist between the habitat associations of penultimate females and those of penultimate males ($X^2 = 4.3$, $P > 0.30$).

Younger spiders primarily occupy the grass substrate associated with the woodland floor. On the other hand, adult spiders are located in the vicinity of the creek (Fig. 2). (A chi square test completed on the quadrat associations of spiders shows adult males and females to be more active in quadrats 1 and 2 and penultimate spiders in 4 and 5 ($X^2 = 8.8$ $P < 0.07$).

This movement toward the creek is further supported by our observations on the movements of marked individuals over an eighteen day period. In a significant number of sightings (Binomial Test, N=85, $P < 0.05$), individual spiders were moving towards the

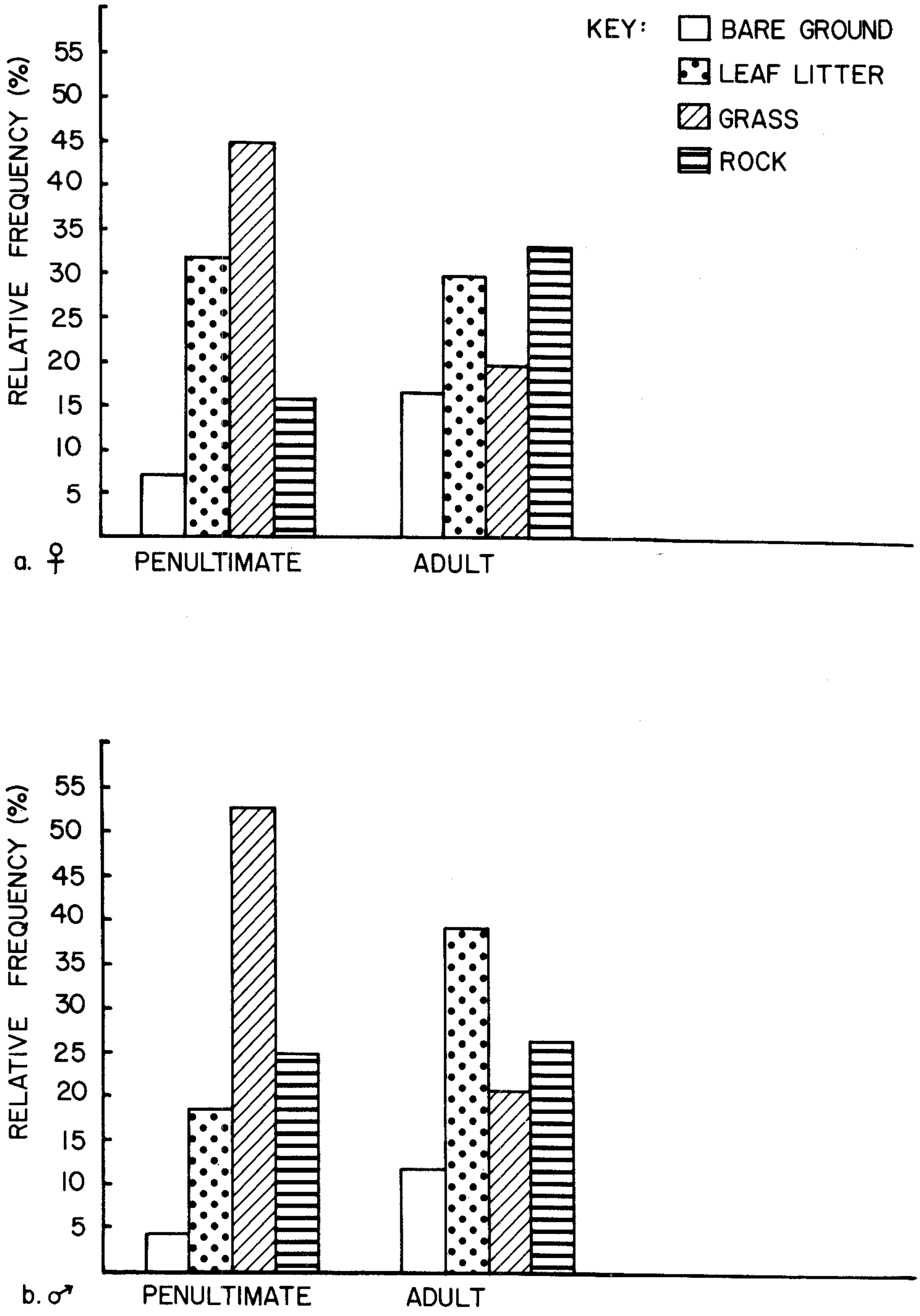

Fig. 1.—Relative frequency of spider associations with (narrow bar), and activity on (wide bar), different substrates: la, females; lb, males.

creek as opposed to away from it. When we consider the additional facts that lycosids are highly mobile and that the distances involved in this study are well within the dispersal capabilities of wolf spiders (Uetz 1976), we must conclude that the results presented here indicate that *Lycosa santrita* is exhibiting active habitat selection.

PREY AVAILABILITY

Riechert (1976) has shown that spider species can detect areas of high prey density and move into them [the aggregational response of Readshaw (1973)]. It is possible that the changes in association with different habitat patches exhibited by *L. santrita* reflect changes in the local abundances of prey and associated moves by these spiders in search of new patches of high prey density. The following experiment was designed to test this hypothesis.

Methods.—Prey availability is herein defined as those prey coming within the detection range of the spider. Balls of chicken coop wire intermeshed with string and coated with a tree banding compound (Stikem Special ^{R}) were used in its estimation. Each ball was 9

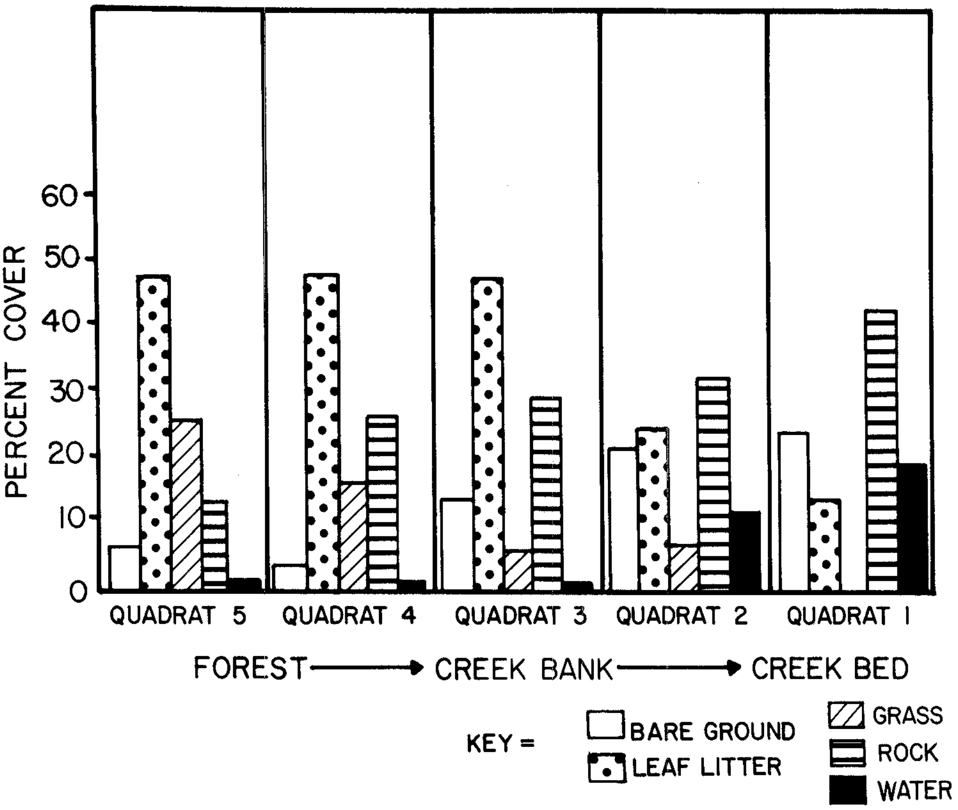

Fig. 2.—Absolute representation (% cover) of various substrates in riparian habitat. Position of sample quadrats relative to creek bed and forest indicated. Quadrats are 1 meter and extend 30 meters parallel to creek bed.

cm in diameter, assuming that the spider was located in the center and could detect prey within a radius of 4.5 cm. [This detection radius was determined through the offering of tethered prey at various distances to stationary spiders in the habitat (Kronk 1976)]. Three balls were placed on each of four substrate types and prey items were collected once every 24 hours for 21 days during August and September of 1975. (Sample adequacy was set as that N which provided a standard error of equal to or less than 10% of mean prey density). The number of prey caught on a ball during the collection period and the total dry weight of these prey were recorded for all samples.

Results.—Analyses of variance computed on the total dry weights and densities of prey associated with specific substrates showed a significant variation to exist (Table 4). The Duncan's multiple range test was then used to determine which substrates differed significantly from each other (Table 5). Prey availability was significantly greater on patches of bare ground than on other substrates. This is not unexpected as bare ground is prominent at the creek edge and insects seeking water can best obtain it from this type of substrate which tends to absorb moisture.

What is unexpected, however, is the observation that differences in prey availability associated with specific substrates were maintained throughout the study period—despite the changes in substrate association exhibited by the spiders during the same time period. This observation comes from comparisons made between the catches from a particular substrate during the first 10 days of the experiment with those from the last 10 days. A Cox and Stuart test for trend (1955) showed no significant differences in prey density or dry weight to exist on any of the substrates between the first half of the sampling period and the second half. Thus, changes in habitat association do not appear to be related to changes in insect abundance.

Table 4a.—Analysis of Variance for Dry Weight of Available Prey (DF = Degrees of Freedom, SS = Sum of Squares, MS = Mean Square).

Source of Variation	DF	SS	MS	F	Tabular F
Total	314	345961.14			
Treatments	4	108124.25	27031.06	11.21	$F_{0.005(4,80)}=4.07$
Replication	20	30522.47	1526.12	0.63	$F_{0.05(20,80)}=1.72$
Rep. X Trt.	80	192965.05	2412.06	35.30	$F_{0.005(80,210)}=1.47$
Error	210	14349.37	68.33		

Table 4b.—Analysis of Variance for Available Prey Density.

Source of Variation	DF	SS	MS	F	Tabular F
Total	314	32214.97			
Treatments	4	9334.24	2333.56	31.56	$F_{0.005(4,80)}=4.07$
Replication	20	5957.37	297.87	4.03	$F_{0.005(20,80)}=2.32$
Rep. X Trt.	80	5916.03	73.95	1.41	$F_{0.025(80,210)}=1.35$
E Error	210	11007.33	52.42		

Table 5.–Results of Multiple Range Tests: (a) for prey weight underlined area indicates values not significantly different from each other ($P > 0.05$). Prey weight is significantly less on rocks, litter, and grass than on bare ground, and less on grass than on rocks and litter; (b) available prey density is significantly different from other substrates on all substrates ($P < 0.05$).

a. For Prey Weight:

	Substrates			
Statistic	Bare Ground	Rock	Litter	Grass
Treatment $\bar{X}$ (mg. dry wt.)	21.4	9.7	8.2	4.3

b. For Prey Density:

Statistic	Bare Ground	Rock	Litter	Grass
Treatment $\bar{X}$ (number)	61.7	36.0	25.9	13.4

DISCUSSION

Numerous factors appear to be influencing *L. santrita's* choice of habitat. These include capture efficiency, energy needs as they vary with age, prey availability, the availability of potential mates and protection from predation. The proposed relationship among these factors is shown in Table 6. Despite the fact that association with areas predominantly covered with grass affords less prey, penultimate spiders inhabit these areas. In doing so, this spider appears to be minimizing uncertain time investments in prey capture. (Grass substrates contain the greatest predictability of capture time for prey located at specific distances from the spider). This time and energy investment is less certain for other substrates wherein the degrees of follow-up search and pursuit required for specific prey at given distances vary markedly. Association with the grass substrate also affords *L. santrita* protection from potential predation by spider wasps (Pompilidae) which are numerically prominent in the study area and are known predators of *L. santrita* (unpublished observations).

The tendency to stay on grass substrates which afford maximum capture efficiency and protection from predation, appears to be overridden by the need of adult female spiders to maximize food intake for the reproductive effort. Females at this time move to the bare ground areas adjacent to the creek bed where prey densities are considerably higher. The necessity of this move is supported by the results of a separate feeding and weight gain experiment with *L. santrita*. Twenty-four penultimate female spiders were collected, weighed and placed in containers covered with cheese cloth. These individuals were fed at one of four feeding levels on alternate days for a three week period. (On non-feeding days, the containers were placed in the study area, exposing the captives to temperatures and humidities experienced under natural conditions). On the final day of

Table 6.–Significance of habitat choice to spiders of different age and sex.

	Juveniles	Adult Females	Adult Males
General Substrate Association	Grass	1) Bare ground	1) Leaf Litter
Location in Habitat	Forest Floor	2) Rock	2) Bare Ground
Property Maximized	Capture Efficiency	Prey Availability	Mating Probability
Property Minimized	Potential Predation		Potential Predation

the experiment, the captives were weighed again, along with 10 newly captured spiders. The prey consumption required for specific weight gains was calculated from the resulting data (Table 7). The dry weight of prey required to realize the weight gain observed in the field at the transition period between the penultimate and adult stage was estimated to be 3.51 mg/day. This weight is available on the grass substrates (Table 5). However, in the experiment we find that the spiders are capable of consuming weights of prey of 17.56 mg/day. These quantities of prey are only available on bare ground substrates in the study area (Table 5).

Grasses, though less prominent in the creek bed are still used by females, when possible, in prey capture. Females also use the rock substrate in the creek area where prey availability is higher than on the grass or adjacent litter substrates though less than on the bare ground (Table 5). Rock affords significantly greater capture efficiency than bare ground (Table 3), and spiders in the vicinity of the creek may prefer it to the bare ground for this reason.

Adult males are known to be erratic in their food consumption (Riechert 1978). It appears unlikely, then, that their move to the creek bed area is related to food needs. Male spiders are most active in the leaf litter adjacent to bare ground and rock patches being utilized by females. They can best avoid predators in this habitat, while their close proximity to the females ensures a chance at mating. (We assume that females also seek shelter in the leaf litter during periods of inactivity).

Additional benefits to the population may result from the habitat selection of adult *L. santrita*. For example, it may minimize competition with juveniles for prey and/or minimize cannibalism of juveniles by adults.

The mechanisms by which these changes in substrate associations might be achieved are known from studies with other spiders. Riechert (1976), for instance, has shown that spiders search for and settle in areas of high prey density. In addition, Edgar (1971) in a study of *L. (Pardosa) lugubris* found that the adults moved to areas of high prey availability and away from areas occupied by younger spiders. *Lycosa santrita* can use the sensory capabilities of its tarsal slit organs to similarly locate areas of abundant prey. The increased hunger levels experienced by the females might provide the stimulus needed to migrate. The move by males to the vicinity of the creek is probably not mediated by prey activity. Rather, males in search of potential mates may follow the dragline silk laid down by females as they move into the creek bank area: experiments completed by Tietjen (1977) show that a pheromone is laid down with the dragline silk of female lycosids and that males actively follow these pheromone trails. Tietjen's (1977) study and a study conducted by Dondale and Hedgekar (1973) suggest that moisture on the bare ground substrate would inactivate the pheromone. Therefore, the pheromonal attraction would be expected to be the greatest on the dry litter located on the creek bank.

Table 7.–Summary of Female *Lycosa santrita* Feeding Dynamics [*Estimates calculated from laboratory results with weight gain in the field setting scale].

Feeding Characteristics	Laboratory Groups (wet wt.)				Field (wet wt.)	Field Equivalent (dry. wt)
$\bar{X}$ mg consumed/day	36.67	20.00	15.00	10.17	7.17*	
$\bar{X}$ mg gained/day	8.33	6.75	3.17	2.20	1.79	
$\bar{X}$ mg prey available/day	99.63	50.95	26.22	13.58	9.81*	3.51
Assimilation Coefficient (mg gained/mg consumed)	.23	.31	.23	.25		
Ingestion Coefficient (mg consumed/mg available)	.66	.72	.73	.74		
Mg prey available/day to optimize consumption					49.32*	17.56

The system of habitat choice described herein is an example of a complex life history in which the particular "strategy" used at a given time changes with age and differs with the sex of the individual. The view the researcher receives at any point in time thus merely reflects the resulting compromise of the many needs and selection pressures impinging upon the individual spider at that time and earlier times in its life cycle. Understanding of the "suite" of adaptations involved in the overall selection strategy requires continued study throughout the life cycle of the species population.

Confusion also exists concerning the relative importance of various components to the life history strategy. Recent studies emphasize such parameters as clutch size, degree of parental investment, longevity etc. (Wilbur et al. 1974, Pianka 1976). Our work suggests that complexities involved in habitat choice are just as important to optimal reproductive success as these other aspects of life histories. Stearns (1977) in his review of the subject concurs.

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LITERATURE CITED

Barth, F. G. 1967. Single slit sensillum on spider tarsus: Its nervous response to the components of airborne sound. Z. Vergl. Physiologie, 55:407-449.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Sci. Amer., 225:86-93.

Bennett, C. A. and J. L. Franklin. 1954. Statistical analysis in chemistry and the chemical industry. New York. John Wiley and Sons.

Carrel, J. E. and R. D. Heathcote. 1976. Heart rate in spiders; influence of body size and foraging energetics. Science, 193:148-150.

Cox, D. R. and A. Stuart. 1955. Some quick tests for trend in location and dispersion. Biometrika, 42:80-95.

Dondale, C. D. and B. M. Hegdekar. 1973. The contact sex pheromone of *Pardosa lapidicina* Emerton (Araneae: Lycosidae). Canadian J. Zool., 51:400-401.

Edgar, W. D. 1971. The life cycle, abundance, and seasonal movements of the wolf spider *Lycosa (Pardosa) lugubris*, in central Scotland. J. Anim. Ecol. 40:303-322.

Gertsch, W. J. and S. E. Riechert. 1976. The spatial and temporal partitioning of a desert spider community with descriptions of new species. Amer. Mus. Novit., 2604.

Gorner, P. and P. Andrews. 1969. Trichobothria organs of 'touch at a distance' in spiders. Z. Vergl. Physiologie, 64:301-317.

Greenquist, E. A. and J. S. Rovner. 1976. Lycosid spiders on artificial foliage: Stratum choice, orientation preferences and prey-wrapping. Psyche, 83:196-209.

Harper, C. A. 1971. Comparative ecology of two sibling species of wolf spiders. Ph.D. Thesis. University of Florida.

Kessler-Geschier, A. M. 1971. Distribution and interspecific competition of congeneric species of spiders in a series of marshy habitats. Proc. Intern. Congress Arachnol., 5:171-178.

Kronk, A. E. 1976. Habitat selection and feeding efficiency of *Lycosa santrita* Chamberlin and Ivie. Masters Thesis. University of Tennessee, Knoxville.

Kronk, A. E. 1976. Feeding and Mobility Characteristics of *Lycosa santrita* Chamberlin and Ivie. Unpublished study.

Lowe, C. H. 1972. The vertebrates of Arizona. Tucson, Arizona. Univ. Arizona Press.

Luczak, J. 1966. The distribution of wandering spiders in different layers of the environment as a result of interspecific competition. Ecol. Polska Ser. A., 14:233-244.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. Amer. Zool., 16:775-784.

Post, W. M. and S. E. Riechert. 1977. Initial investigation into the structure of spider communities. I. Competitive effects. J. Anim. Ecol., 46:729-749.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol., 52:137-154.

Readshaw, J. L. 1973. The numerical response of predators to prey density. J. Appl. Ecol., 10:342-351.

Riechert, S. E. 1978. Energy-based territoriality in populations of the desert spider *Agelenopsis aperta* (Gertsch). Symp. Zool. Soc. London, 42:211-222.

Riechert, S. E. 1976. Web-site selection in a desert spider. Oikos, 27:311-315.

Riechert, S. E. and C. R. Tracy. 1975. Thermal balance and prey availability: Bases for a model relating web-site characteristics to spider reproductive success. Ecology, 56:265-284.

Schaefer, M. 1975. Experimental studies on the importance of interspecies competition for the lycosid spiders in a salt marsh. Proc. 6th Int. Congress Arachnol., 86-90.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Ames, Iowa. Iowa State Univ. Press.

Stearns, S. C. 1977. The evolution of life history traits. Ann. Rev. Ecol. Syst., 8:145-172.

Tietjen, W. J. 1977. Dragline-following by male lycosid spiders. Psyche, 84:165-178.

Tretzel, E. 1955. Intragenerische Isolation and Interspezifische Konkurrenz bei Spinnen. Z. Morphol. Oekol. Tiere, 44:43-162.

Turnbull, A. L. 1964. The search for prey by a web-building spider *Achaearanea tepidoriorum* (C. L. Koch) (Araneae, Theridiidae). Canadian Entomol., 96:568-596.

Uetz, G. W. 1976. Gradient analysis of spider communities in a streamside forest. Oecologia, 22:373-385.

Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Amer. Nat., 108:808-817.