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THE MECHANISM OF HABITAT SELECTION IN THE LONG-JAWED ORB-WEAVING SPIDER *TETRAGNATHA ELONGATA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT

Tetragnatha elongata is associated exclusively with riparian habitats. The physiological suitability of a given environment is determined by accessibility to open water. When this is denied, spiders suffer dehydration, the rate of which is determined by the temperature and relative humidity. Where the abiotic environment is suitable, spiders build webs on any available structural support. The webs of *T. elongata* are short lived. Once a web has been built, a spider may rebuild at the same site or move to a new site. Prey availability appears to be the primary determinant as to which of these alternatives is adopted.

INTRODUCTION

One of the most important decisions web-building spiders make during their life is that of selecting a site in which to build. These decisions are known to strongly influence spider growth, survival and reproduction (Riechert and Tracy 1975). Habitat utilization has been described in a large number of spiders, strong associations being found with abiotic factors such as structural features, temperature, wind, rain and humidity; similar associations have been found with areas of high prey availability (Riechert and Gillespie 1986). Such associations need not, however, imply habitat selection: ballooning may allow spiders to be carried to different areas using wind currents. But, as shown by Tolbert (1976), spiderlings may reinitiate ballooning, presumably after sampling the local environment encountered following initial dispersal. Changing environmental conditions have also been found to cue dispersal in later life history stages in, for example, linyphiids (Duffey 1956, 1963, Wingerden and Vughts 1974, Vughts and Wingerden 1976). Chance encounter is therefore insufficient to account for the habitat ultimately occupied by these spiders.

A number of spider species have also been shown to exhibit active preference for a specific abiotic environment reflective of their natural habitat (Norgaard 1951, Cloudsley-Thompson 1957, Riechert 1976). Similarly, several groups have been shown to exhibit active site selection on the basis of prey availability

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(Turnbull 1964, Dabrowska Prot et al. 1968, Holldobler 1970, Luczak 1970, Riechert 1976, Gillespie 1981, MacKay 1982, Morse & Fritz 1982, Olive 1982). In this paper I examine the extent to which habitat utilization involves active site selection, using the long-jawed orb-weaving spider *Tetragnatha elongata* Walckenaer (Levi 1981). This species, in common with other tetragnathids, builds delicate, short-lived orb webs which are taken down and ingested daily if not more frequently. Webs are built by immatures and mature females. *T. elongata* is associated exclusively with aquatic habitats. The present study was conducted in North Carolina during the summers of 1982-1984. I first looked at the distributional pattern of the spiders—the organization of a population through the spatial arrangement of its individuals in the environment (Pielou 1969). The technique used was the same as that employed to examine the patterns of distribution of the desert funnel-web spider *Agelenopsis aperta* (Gertsch) (Riechert et al. 1973; Riechert 1974). The second part of this study examines whether the observed pattern of distribution is a consequence of differential survival, or is rather caused by active habitat selection.

METHODS

Two study areas were established in the vicinity of Highlands Biological Station in western North Carolina. The first was in a cool, sheltered woodern with a creek. The other was an exposed area near the edge of a lake where dead twigs and branches jut out of the water.

Pattern.—*Field Methods.* Two plots—one on the creek (64 m x 16 m) and the other on the lake (16 m x 16 m)—were selected and mapped in July 1982. Plot sizes were selected in order to include comparable areas (approx. 25 m^2) of surface water in the different habitats. Each plot was divided into quadrats of 1.0 m^2 for mapping. Webs on the creek were examined, and their location within a quadrat recorded, over a period of 32 days. An index of web site suitability was obtained by using the frequency with which each site was used over this period. Webs on the lake were far more dense. Data on web locations here were taken from censuses on two consecutive days, during which time approximately the same number of webs were recorded as in the creek habitat. In each plot, the distribution of habitat features and microclimate characteristics were also mapped. Measurements were then taken in each quadrat of: water, sand, moss and leaf litter; twigs (branches less than 2 cm diameter) and branches (more than 2 cm diameter) at heights of 0-50 cm, 50 cm-1 m, 1-2 m and 2-4 m. Microclimate characteristics (light intensity, temperature, humidity, wind speed and water flow rate) were also measured on three occasions (each on clear, sunny days) in each plot.

Methods of Analysis. Block size analysis of variance was used to examine the distribution of webs in the study areas. This type of pattern analysis was developed by Greig-Smith (1952, 1961, 1964) and Kershaw (1960, 1964) for measuring departure from randomness. It is useful in dealing with most natural situations in which not only presence or absence are involved but also ranges of density (Greig-Smith 1961). Covariance was calculated between web distribution and that of each of the habitat features mentioned above in all plots. This allowed the determination of pattern scales as well as significant associations.

Factors responsible for survival and web building.—In order to determine whether *T. elongata* was exhibiting active selection of web sites, it was necessary to examine (1) those parameters which allowed survival; (2) those required for construction of the web trap; and (3) the probability that a spider would move from a site where it had built a web versus situations where no web was built. The variables I chose to examine (on the basis of the results from the pattern analysis) were: (1) temperature (2) light intensity (3) humidity (4) presence of open water and (5) prey availability. Within its natural distributional area, the parameter most likely to have an immediate effect on individual survival is desiccation (caused by high temperature, low humidity or the absence of water). The relative effects of each of these parameters was measured through a series of experiments (Table 1): A, high temperature, low humidity, no water; B, high temperature, high humidity, water present; C, high temperature, high humidity, no water; D, lower temperature, low humidity, no water; E, lower temperature, high humidity, water present; F, lower temperature, high humidity, no water. For each treatment (A-F) six spiders were used. After being weighed, individuals were placed in small, cylindrical, plastic vials (height 5 cm, diameter 2.5 cm) covered with cheesecloth. The weight of each spider was recorded at quarter hour intervals during a 10 hour treatment. For spiders that died, recordings were taken up until death.

The most likely parameters to exert a direct effect on web-building behavior in *T. elongata* were considered to be one or more of the following: (1) vulnerability to desiccation (i.e. the combined effects of temperature, humidity and open water); (2) light intensity (acting as a cue to humidity) and (3) prey availability. Results from the tests on survivorship (Table 1) showed that direct access to open water was needed to prevent desiccation. Field cage experimentation was used to examine this. Two cages were set up—identical except that the floor of one was covered with wire mesh (to allow the passage of small emergent aquatic insects, but prevent direct access to the water by spiders); the other was open to the water's surface. These cages were 1.5 m x 0.6 m x 0.6 m, and were placed at the same orientation (with respect to incident sunlight), separated by a distance of approximately 2 m. The sides were covered with clear polythene and the top with fine wire netting. Wooden bars crisscrossed the cages to provide structural support. The effects of incident solar radiation were examined by dividing each of the cages into two equal portions along their length by means of a polythene sheet. One of these sections in each cage was covered with aluminum foil and black polyethelene to block out a large portion of both visible and infrared wavelengths of the solar spectrum. Any time that measurements were made on the spiders, recordings were taken of temperature (°C) and illuminescence (lumens m^{-2}) in both covered and open sections of the cages. In order to control for any differences in these variables that might exist between the two cages, recordings were taken from both at approximately the same time. Humidity was also measured.

Two separate experimental procedures were employed to examine the respective effects of desiccation and light intensity on web-building. In the first, a total of 12 adult female spiders were collected, weighed and marked, and six were placed in each section on a clear, sunny day. Individuals were weighed hourly from 0600 to 2100 h. (To do this, in order to minimize time out of the cage, spiders were taken in rotation.) The experiment was replicated on the next clear,

Table 1.—Set of experiments to test survivorship under various extremes of the abiotic environment: Weighed spiders were placed individually in small cylindrical vials (height 5 cm, diameter 2.5 cm) covered with cheesecloth, and were then subjected to one of six treatments. Water (up to 5 mm in the vial) was added to four of the vials, but was covered over with wire mesh (to prevent direct access by the spider) in two of these. Half the vials were placed in a desiccator (temperature 37.5°C, humidity 4%) and the other half were kept in the laboratory (temperature 18.0°C, humidity 75%). Six spiders were tested under each of these sets of conditions.

	TREATMENT					
	A	B	C	D	E	F
TEMPERATURE	37.5	37.5	37.5	18.0	18.0	18.0
ACCESSIBILITY OF OPEN WATER	NO	YES	NO	NO	YES	NO
HUMIDITY	4%	75%	75%	4%	75%	75%
EXPERIMENTAL SET UP						
Desiccator	yes	yes	yes	no	no	no
Water	none	present	covered	none	present	covered

sunny day with 12 new spiders. In the second experiment, 12 new spiders were collected and six weighed and marked individuals placed, as before, in each section. Spider activity and web lifespan were monitored at hourly intervals each day for a 16-day period. The procedure was replicated over the next 16 days.

In order to determine the effect of prey availability on web-building, a series of small cages (39.3 cm x 39.3 cm x 11.4 cm) were set up along a stream bed, where the incidence of solar radiation was very low (midday peak approx. 37.20 lumens m^{-2}). Individual spiders were weighed and then placed in these cages, where they had direct access to open water. The spiders were fed on field-collected fruit flies (*Drosophila* spp.) caught from a culture of rotten fruit just prior to feeding. Spiders were fed at 2000 h daily, insects being placed in the cages by means of specifically designed apertures in their tops. The stoppers in these apertures were removed, and tubes containing the insects inverted over the top. Although the presence of soft tissue paper in the tubes prevented the insects from just dropping into the water, prey capture success was low: spiders caught approximately 30% of the insects administered. The tubes were left in the inverted position until the next day. In order to find the relationship between prey availability and web-building, spiders were subjected to one of three treatments for a period of ten days: insects administered at a rate of 20, 5 and 0. The extent to which web-building occurs in the absence of any stimuli from either light or prey was examined by daily monitoring of spiders in a dark room without insects (six weighed spiders in a 1.2 m x 0.6 m x 0.5 m cage placed in a basin of water).

Finally, the probability that a spider would move from a site where it had built a web versus a situation where no web was built, was examined using a wood-framed cage (1.2 m x 1.2 m x 0.6 m high) with clear plastic sides and provided with wooden struts for web-building. The top was covered with cheesecloth and the bottom was open to the surface of a shallow pool of water. Eight marked spiders were placed in the cage and monitored throughout the season by recording the number of webs, mapping their specific locations and noting the identity of the spider occupant every day. This allowed a comparison of the numbers that changed site subsequent to building versus those that moved from a site where no web was built.

RESULTS

Pattern.—Analysis of web pattern showed *T. elongata* to be associated exclusively with areas of open water, provided that suitable structural supports (twigs, branches, etc.) are available (Table 2). Comparing the two habitats used in the study, webs were found to be more intimately associated with twigs on the lake, which reflects the higher web density in this population. Neither habitat exhibited significant associations of webs with other abiotic features measured such as light intensity, temperature, humidity or wind speed.

Factors responsible for survival and web building.—The results from experiments to determine the effect of abiotic parameters on survival are shown in Table 3. Spiders were found to tolerate a maximum dehydration weight loss of approximately 15%. The rate of desiccation appears to be more a function of temperature than humidity, although the rate of weight loss was considerably reduced at high humidities. In any situation where spiders are denied direct access to water, however, desiccation appears to occur. But, even at high temperatures, virtually no weight loss was detected if individuals had direct access to open water.

The water loss suffered at different times of the day, and—at corresponding times—the effect of light intensity and temperature on web-building is shown in Table 4 for situations where water is, and where it is not, accessible. The primary determinant of web-building appears to be access to open water. When they cannot reach water, spiders suffer desiccation (the rate of which is determined by the temperature) and never build webs. Light intensity, although it does not appear to exert a significant effect on the presence of a web, does determine the activity pattern of the spider: at high light intensities spiders move off the hub of the orb. They do, however, continue to monitor prey impinging on the orb through tarsal contact with one of the bridge lines.

Total movement was also documented by recording the position of individuals in the uncovered (illuminated) sections of both cages each day. The average distance moved by an individual on any given day (averaged over 6 days) was found to be 74.0 cm in the cage with the bottom covered, and 29.6cm in the cage providing accessibility to open water (*t-test:* $t = 18.41$, $p < 0.01$). The effect of prey availability on web-building was determined by counting the number of days on which webs were built for each spider. Results (Table 5) showed tht spiders

Table 2.— Spider web associations: Correlation coefficients were computed on covariance between the distribution of webs and that of habitat features and microclimate characteristics on both the creek and the lake. The following associations were found to be significant (* : $p < 0.05$; ** : $p < 0.01$).

	CREEK	LAKE
WATER	**	**
MOSS	*	
BRANCHES Low, 0-50 cm		**
Middle, 50-100 cm	*	*
TWIGS Low, 0-50 cm	*	**
Middle, 50-100 cm	*	**
High, 100-200 cm		**

Table 3.—The effect of temperature, humidity and open water on dehydration of spiders: Individual spiders (n = 36) were subjected to one of six treatments (see Table 1). Water (height 5 mm up vial of height 5 cm) was placed in four of the vials, but was covered over (to prevent direct access by the spider) in two of these. Half the vials were kept in a desiccator (temperature 37.5°C, humidity 4%); the other half in the laboratory (temperature 18.0°C, humidity 75%). The weight of each spider was recorded at quarter hourly intervals during each 10 hour treatment, and allowed an estimate of the rate of desiccation shown here (mean, SD), along with the original weight of the spider (mean, SD). The weight loss suffered by spiders just prior to death allowed estimation of the % weight loss tolerated.

TREATMENT	DESICCATION RATE (wt.loss,mg/h) (mean, SD)	INITIAL WT. (mg) (mean, SD)	%WT.LOSS before death (mean, SD)
High temperature, low humidity, no water.	5.15 (±0.66)	56.13 (±14.51)	14.82 (±2.81)
High temperature, high humidity, no water.	4.42 (±0.83)	59.30 (±13.95)	15.12 (±1.01)
High temperature, high humidity, open water.	0.05 (±0.05)	60.93 (±13.59)	—
Low temperature, low humidity, no water.	0.13 (±0.05)	55.80 (±12.65)	—
Low temperature, high humidity, no water.	0.21 (±0.10)	60.35 (±11.58)	—
Low temperature, high humidity, open water.	0.00	64.08 (±13.92)	—

would generally build webs daily when administered 20 flies a day. At very low prey administration levels (five or zero) web-building frequency was found to drop sharply, though even when prey were absent spiders still built orbs, albeit at a very low frequency. Indeed, where spiders were deprived of all external stimuli, webs were still built, though very infrequently: of six spiders, only four webs were built (by different spiders) over a ten-day period; none of these were maintained for more than 1.5 days (average 1.25 days).

The final experiment was a comparison of translocation frequency in spiders that had built webs versus those that moved from a site where they had not built. This showed that 27% of spiders (n = 132) would move after they had built an orb. On the other hand, of those that did not build orbs (n = 187) 83% moved.

DISCUSSION

The results from this study show: (1) The pattern of distribution of *T. elongata* is non-random, spiders being found to be positively associated with areas over water that are suitable for web-building. (2) In terms of abiotic parameters, the ability of a spider to survive in a given environment is determined by the rate of desiccation, this being a function of humidity and temperature. The effects of desiccation can be counteracted by access to open water. (3) Where abiotic

Table 4.—Daily variation in water loss, light intensity, web-building and occupation of the hub of an orb where water is and is not accessible.

			WATER ACCESSIBLE		WATER NOT ACCESSIBLE	
TIME (hrs)	Mean light reading (lumens/m²)	Mean temp. °C	Mean water loss(mg)	% at hub (mean web #=2.8±0.5)	Mean water loss(mg)	% at hub: # webs built
0600	—	0.00	—	100	11.0	—
0900	0.08	5.58	0	73	14.5	—
1200	0.34	6.05	0	70	19.5	—
1500	0.46	5.58	0	74	19.0	—
1800	0.21	3.72	0	80	19.0	—
2100	0.02	0.00	0	100	17.0	—
0600	—	0.00	—	100	11.0	—
0900	0.06	46.50	0	0	20.0	—
1200	5.34	186.00	0	0	29.5	—
1500	4.42	186.00	0	0	28.5	—
1800	2.83	65.10	0	0	19.0	—
2100	0.00	1.86	0	0	17.0	—

conditions are suitable, spiders will build orbs on a daily basis provided there is adequate prey available. (4) The probability of changing site is much higher where no web has been built. A three component mechanism of habitat selection in *T. elongata* may occur as spiders operate by the parameters identified in this study. (1) Random movement curtailed upon encountering a favorable abiotic environment. Alternatively, if they do not move, temporal variability may cause the environment surrounding the spider to change. The end result of either spatial or temporal change might trigger off (2) active search for a specific microhabitat within this environment which satisfies the requirements for web construction. (3) Site sampling occurs once the web has been built and leads to a repetition of the process if the spider's immediate foraging requirements necessary for survival are not satisfied. (*T. elongata* loses weight and will die when administered prey at a level much below 10 per day; see Gillespie and Caraco, in press).

The first component—the random search phase—has been recognized and described in a number of spider groups (Riechert and Gillespie 1986). The mechanism behind this procedure has been considered in terms of negative feedback (Sale 1969): where the environment is inadequate, low intensity feedback causes a high level of exploratory activity. As shown in this study, *T. elongata* does not build webs where the environment is unfavorable (i.e. there is no open water accessible). During this period, their activity may be largely non-directed exploratory movement, which would frequently enable them to locate a suitable environment. It may be that a similar mechanism is used by other species that are associated with specific forms and strata of vegetation that permit efficient perception and capture of prey (Hallander 1967, 1970, Kronk and Riechert 1979).

The second component involves active search for a specific microhabitat. The importance of spatial/architectural features of the habitat in determining the specific location of webs has been documented in araneids (Colebourn 1974) and linyphiids (Schaefer 1978). In this study, twigs appeared to be the structures of primary necessity for web-building in *T. elongata*. LeSar and Unzicker (1978), working with the closely related *T. laboriosa*, came to similar conclusions.

Table 5.—The effect of prey availability on web-building.

TREATMENT (No. of insects)	AV. NO. WEBS BUILT (Mean & C.L.: taken over 10 day period)	NO. SPIDERS USED
20	10.92 (±1.33)	18
5	3.75 (±1.88)	9
0	1.28 (±0.53)	16

The final component considered to be involved in the habitat selection process of *T. elongata* is web relocation if the insect availability is insufficient to allow survival (Gillespie and Caraco, in press). It differs from the first component of random search in that it cannot be explained by the idea of negative feedback (Sale 1969). Rather, it is a continual trial and error procedure. Also, due to the effect of temporal variation superimposed on spatial variation, no one site can be optimal for any length of time. This component of the habitat selection process has been documented in many species that require web traps to be built before they can estimate the availability of prey in particular patches. Hildrew and Townsend (1980) report this type of behavior in the caddis fly larva *Plectrocnemia conspersa*. Amongst spiders, Turnbull (1964) found that individuals of the house spider *Achaearanea tepidariorum* (C. L. Koch), when released into an empty room, will continue to change web locations until all have built webs in the vicinity of a localized prey source (in this case a window, where flies were attracted to the light). In two studies on theridiid ant specialists, a change in web location has been shown to be associated with predation avoidance tactics of the ants: Holldobler (1970) noted that *Steatoda fulva* (Keyserling) changes web location from one ant mound to another following cessation of ant usage of particular entrances. MacKay (1982) found that *Latrodectus hesperus* Chamberlin and Ivie migrates from a nest of ants that have ceased to forage. The crab spider *Misumena vatia* (Clerck) leaves flowers that yield insufficient prey (Morse and Fritz 1982). And amongst tetragnathids, *T. montana* Simon has been shown to base its web-building activity on mosquito abundance (Dabrowska Prot et al. 1968, Luczak 1970). Olive (1982) has shown that this process of web relocation occurs when the current rations a spider is receiving fall below its previous rations, and the effect of this tendency is aggregation of animals in quadrats with high ration levels.

This type of three-component sequence of habitat selection may well explain the mechanism by which a suitable habitat is located by most web-building spiders. The method of prey sampling will, however, vary depending on web investment at any given site (Rypstra 1983). Spiders with a high investment are unlikely to build complete webs to sample prey availability, as the cost incurred by such behavior would be inordinately high. Gillespie (1981) showed that the cribellate spider *Amaurobius similis* (Blackwall) (which has a very high web investment) continually lays single silk threads during the sampling period. This may be the standard sampling technique used when web investment is high.

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LITERATURE CITED

Cloudsley-Thompson, J. L. 1957. Studies in diurnal rhythms V: Nocturnal ecology and water relations of the British cribellate spiders of the genus *Ciniflo*. J. Linnean Soc. Zool., 43:134-152.

Colebourn, P. H. 1974. The influence of habitat structure on the distribution of *Araneus diadematus* Clerck. J. Anim. Ecol., 43:401-409.

Dabrowska Prot, E., J. Luczak, and K. Tarwid 1968. Prey and predator density and their reactions in the process of mosquito reduction by spiders in field experiments. Ekologia Polska—Seria A, 16(40):773-819.

Duffey, E. 1956. Aerial dispersal in a known spider population. J. Anim. Ecol., 25:85-111.

Duffey, E. 1963. A mass dispersal of spiders. Trans. Norfolk Norwich Natur. Soc., 20:38-45.

Gillespie, R. G. 1981. The quest for prey by the web building spider *Amaurobius similis* (Blackwell). Anim. Behav., 29:953-954.

Gillespie, R. G. and T. Caraco. In press. Risk-sensitive foraging strategies of two spider populations. Ecology.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of structure of plant communities. Ann. Bot. N. S., 16:293-316.

Greig-Smith, P. 1961. Data on pattern within plant communities. I. The analysis of pattern. J. Ecol., 49:695-702.

Greig-Smith, P. 1964. Quantitative Plant Ecology. 2nd Ed. Butterworth, London.

Hallander, H. 1967. Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O. F. Muller). Oikos, 18:145-150

Hallander, H. 1970. Prey, cannibalism and microhabitat selection in the wolf spider *Pardosa chelata* O. F. Muller and *P. Pullata* Clerck. Oikos, 21:337-340.

Hildrew, A. G. and C. R. Townsend. 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). Anim. Behav., 28:553-560.

Holldobler, B. 1970. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. Psyche, 77:202-208.

Kershaw, K. A. 1960. The detection of pattern and association. J. Ecol., 48:233-242.

Kershaw, K. A. 1964. Quantitative and dynamic ecology. Edward Arnold, London.

Kronk, A. W. and S. E. Riechert. 1979. Parameters affecting the habitat choice of *Lycosa santrita* Chamberlin and Ivie. J. Arachnol., 7:155-166.

LeSar, C. D. and Unzicker, J. D. 1978. Life history, habits and prey preferences of *Tetragnatha laboriosa*. Env. Entomol., 7:879-884.

Levi, H. W. 1981. The American orb weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). Bull. Mus. Comp. Zool., 149(5):271-318.

Luczak, J. 1970. Behaviour of spider populations in the presence of mosquitos. Ekologia Polska, 18(31):625-634.

MacKay, W. P. 1982. The effect of predation of western widow spiders (Araneae: Theridiidae) on harvester ants (Hymenoptera: Formicidae). Oecologia (Berl), 53:404-411.

Morse, D. H. and R. S. Fritz. 1982. Experimental and observational studies of patch choice at different scales by the crab spider, *Misumenta vatia*. Ecology, 63(1):172-182.

Norgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. Oikos, 3(1):1-21.

Olive, C. W. 1982. Behavioral response of a sit and wait predator to spatial variation in foraging gain. Ecology, 63(4):912-920.

Pielou, E. C. 1969. Introduction to Mathematical Ecology. Wiley Interscience, New York.

Riechert, S. E. 1974. The pattern of local web distribution in a desert spider: Mechanisms and seasonal variation. J. Anim. Ecol., 43:733-746.

Richert, S. E. 1976. Web site selection in the desert spider *Agelenopsis aperta*. Oikos, 27:311-315.

Riechert, S. E. and R. G. Gillespie. 1986. Habitat choice and utilization in the web spinners. Pp. 23-48, *In* Spiders-Webs, Behavior, and Evolution. (W. A. Shear, ed.). Stanford Univ. Press. Stanford.

Riechert, S. E., W. G. Reeder and T. A. Allen. 1973. Patterns of spider distribution (*Agelenopsis aperta* (Gertsch)) in desert grassland and recent lava bed habitats, S. central New Mexico. J. Anim. Ecol., 42:19-25.

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(2):265-284.

Rypstra, A. L. 1983. The importance of food and space in limiting web spider densities; a test using field enclosures. Oecologia (Berl.), 59:312-316.

Sale, P. F. 1969. A suggested mechanism for habitat selection by the juvenile Manini, *Acanthurus triostegus sandvicensis* (Streets). Behaviour, 35:27-44.

Schaefer, M. 1978. Some experiments on the regulation of population density in the spider *Floronia bucculenta* (Araneae: Linyphiidae). Symp. Zool. Soc. London, 42:203-210.

Tolbert, W. W. 1976. Population dynamics of the orb weaving spiders *Argiope trifasciata* and *Argiope aurantia* (Araneae: Araneidae): density changes associated with mortality, natality and migrations. Ph.D. diss., Univ. of Tennessee, Knoxville.

Turnbull, A. L. 1964. The search for prey by the web building spider *Achaearanea tepidariorum* (C. L. Koch) (Araneae: Theridiidae). Canadian Entomol., 96:568-579.

Vughts, H. F. and W. K. R. E. van Wingerden. 1976. Meteorological aspects of aeronautic behavior in spiders. Oikos, 27:433-444.

Wingerden, W. K. R. E. van and H. F. Vughts. 1974. Factors influencing aeronautic behaviour in spiders. Bull. British Arachnol. Soc., 3(1):6-10.

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